SB761
.U7N6
#00-11

United States
Department
Of Agriculture

Forest Service

State and Private Forestry

Forest Health Protection

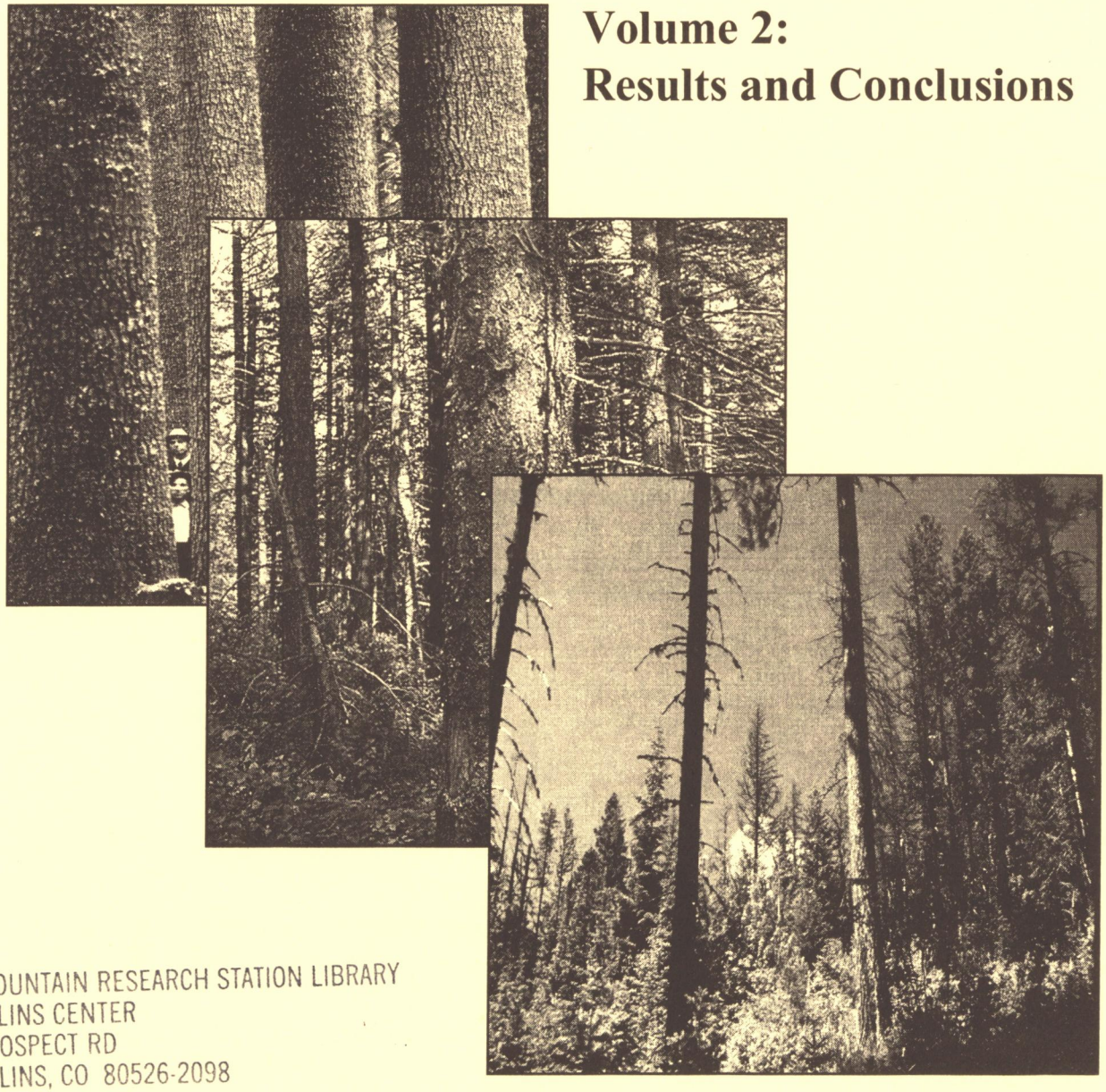
Northern Region

FHP Report No. 00-11

July 2000

Successional Functions of Pathogens and Insects

Ecoregion Sections M332a and M333d in Northern Idaho and Western Montana



Volume 2: Results and Conclusions

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On the cover:

Pathogen and insect succession functions at work through time.

Mountain pine beetle was an important native insect in mature white pine forests (upper-left photograph). With the introduction of the exotic white pine blister rust fungus, white pines were no longer able to survive in great numbers and their place was filled, in large part, by Douglas-fir and grand fir (middle photograph). These forests, in turn, became hosts to epidemics of bark beetles and root diseases. In the aftermath of these epidemics, some forests have been maintained in conditions of perpetually young trees that die from root disease before reaching maturity (lower-right photograph).

Succession Functions of Forest Pathogens and Insects

Ecosections M332a and M333d in
Northern Idaho and Western Montana.

Volume 2: Results

Susan K. Hagle, John W. Schwandt, Terri L. Johnson,
Sandra J. Kegley, Carol S. Bell Randall, Jane E. Taylor,
I. Blakey Lockman, Nancy J. Sturdevant
USDA Forest Service
Cooperative Forestry-Forest Health Protection
Northern Region

Michael A. Marsden
Autometric Service Company

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SECTION 5: RESULTS
Part 1: Vegetation Conditions and Trends

By Susan Hagle

ECOSECTION M332A

Sample Location

Ecosection M332a, the Idaho Batholith Ecosection, includes the southern half of north Idaho and a segment of southwestern Montana (see Figure 2.1) with a significant portion extending into Region 4. Most of the Nez Perce National Forest (NF), the southern half of the Clearwater NF, western half of the Bitterroot NF, and a small part of Lolo NF were sampled within ecosection M332a (Table 5.1).

Table 5.1: National Forest land in sample of ecosection M332a.

National Forest	Hectares in Sample	Percent of Sample
Nez Perce NF	3536.3	43
Bitterroot NF	2634.6	32
Clearwater NF	1873.6	23
Lolo NF	90.1	1

1975-era Polygon Sample

Management history. There had been relatively little tree harvest activity in the sample polygons before the 1975 era. Nine percent of the polygons were identified as having any indication of harvest activity. The few polygons with evidence of harvest activity were insufficient to represent effects of management on succession so they were excluded from further analysis. Fire exclusion probably did affect some of the area that remained in our sample base, however; particularly on the drier, more fire-prone sites. For the most part the changes seen on sites was attributed to natural succession, including the actions of pathogens and insects.

Habitat types. Several habitat type groups were about equal in representation in the sample for M332a (Table 5.2). Group 5 was somewhat more common that the other major types; represented entirely by *Thuja plicata/Clintonia uniflora.* Also quite common in the M332a sample were the moderately warm and dry types (group 2). Here, there were a number of habitat types but *Pseudotsuga menziesii/Physocarpus malvaceus* was particularly common (41 percent of hectares in habitat type group 2). Habitat type *Abies lasiocarpa/C. uniflora* (39 percent of sample hectares) and *A.lasiocarpa/Menziesia ferruginea* (49 percent of hectares) were the most common types in group 7. The sample of group 9 was dominated by *A. lasiocarpa/Xerophyllum tenax* (97 percent of hectares). Habitat type groups that were insufficiently represented to allow characterization of the pathogen and insect functions included: 6, 8, 11, and 15. *P. menziesii/Agropyron spicatum* made up most of the sample in group 1 (48 percent of hectares in

group 1). In most cases, these polygons also had Douglas-fir and ponderosa pine-mixed cover type. The range of possible conditions that were sampled in group 1 was narrow. However, these conditions are represented by a sufficient number of polygons to allow identification of their important pathogen and insect functions. In group 10, *A. lasiocarpa/Luzula hitchcockii* (55 percent of hectares) and *A. lasiocarpa/Vaccinium scoparium* (45 percent of hectares) habitat types were represented. In group 11, *Pinus albicaulis-A. lasiocarpa* (90 percent of hectares) habitat types were well represented. Although groups 10 and 11 were not sufficiently represented to characterize the groups, the habitat type *A. lasiocarpa/L. hitchcockii*, *A. lasiocarpa/V. scoparium*, and *P. albicaulis-A. lasiocarpa* were probably sampled adequately to characterize pathogen and insect functions in major cover types within these habitat types.

Table 5.2: Habitat type groups represented in the 8135 hectares of sample polygons for ecosection M332a.

Group Number	Habitat Type Group	Hectares of Sample	Percent of Sample
1	Warm/dry	526	6
2	Moderately warm/dry	1795	22
3	Moderately warm/moderately dry	738	9
4	Moderately warm/moist	974	12
5	Moderately cool/moist	1292	16
6	Moderately cool/wet	8	0
7	Cool/moist	1012	12
8	Cool/wet	62	1
9	Cool/moderately dry	1238	15
10	Cold/moderately dry	323	4
11	Cold	158	2
15	Grassland/steppe	8	0

Forest types. There were 57 unique forest types assigned. The best-represented forest types are presented in Table 5.3.

Table 5.3: The top 10 forest types in 8,135-hectare sample of M332a in the 1975 era.

Forest Type	Hectares in Sample	Percent of Sample
DF	1418	17
DFPP	700	9
LP	540	7
PP	468	6
GF	450	6
DFGF	419	5
AFLPS	417	5
NF	329	4
C GF	245	3
C	239	3

Douglas-fir was by far the most common single forest type as well as the most common component in combination forest types. Overall 53 percent of hectares in the 1975 sample had forest types with Douglas-fir listed as at least part of the forest type. Grand fir (27 percent), subalpine fir (22 percent), and lodgepole pine (21 percent) were also common in combination or single forest types. In contrast, whitebark pine was listed in only 2 percent of forest types, and western white pine was not listed in any of the 1975 forest types.

Structure classes. Relatively little of the sample area was in a non-forested structure class such as shrubs or grass in the 1975-era data (Table 5.4). Large-tree stands with good density (structure class 3) were most common, followed closely by large-tree stands with poor to moderate density (structure class 4). As expected, the majority of the large-tree structure classes were seen on the most productive habitat types in groups 2, 3, 4, and 5. Pole stands with moderate to good density were commonly produced on the cooler, drier sites typically dominated by subalpine fir and lodgepole pine.

Table 5.4: Distribution of structure classes in the M332a sample in the 1975 and 1935 eras.

Structure Class	Description	% 1935	1935 ha.	% 1975	1975 ha.
0	Non-forested	8	479	3	283
1	Seedling/sapling	7	448	13	804
2	Pole; moderately to well-stocked	41	2,577	27	1,916
3	Large tree; well-stocked	10	646	27	2,048
4	Large tree; poorly to moderately-stocked	34	2,165	30	1,873

Age related to structure classes. Stand age can be calculated in a number of ways with varying results. To get a general idea of how stand age related to polygon structure classes (SC), stand age was calculated as by basal area-weighted tree ages, which were then weighted by polygon hectares. The result is a general indication of the representative age of structure classes (Table 5.5). Polygons with SC 3 were consistently older than those with SC 4, on average, within habitat type groups as well.

Table 5.5: Relationship of average age structure classes and proportion of structure classes 3 and 4 by bd.ft./acre live timber volume classes. Habitat type groups 2, 3, 4 and 5 in M332a.

		Proportion of SC in each bd.ft./acre class (*1000 bd.ft.)					
Structure Class	Age	0-10*	10-20	20-30	30-40	40-50	50+
0	26**	1.00					
1	39	1.00					
2	63	0.48	0.35	0.14	0.02		
3	114	0.01	0.19	0.34	0.35	0.04	0.05
4	102	0.45	0.55	0.00	0.00	0.00	0.00

** The high weighted average ages in structure class 0 results from the presence of very few large, old trees in some polygons with too little total basal area or trees per hectare to qualify as "forested".

Timber volume related to structure classes. Within the habitat types (HT) and structure classes that were expected to have the greatest timber volumes, HT groups 2, 3, 4 and 5 and SC 3 and 4, few stands had timber volumes that the sites are considered capable of producing. Only 13 percent of the sample area of M332a in HT groups 2, 3, 4 and 5 with SC 3 had in excess of 40,000 bd.ft./acre. Stands in structure class 4 did not exceed 20,000 bd.ft./acre, despite averaging 102 years of age.

Polygon Classes Based on Forest Type

The combinations of habitat type groups, forest types, and structure classes represented in the sample resulted in 226 unique polygon classes in M332a. None of the polygon classes represented more that 3.7 percent of the sample area (Table 5.6). There were a few classes which represented a fairly high proportion of the habitat type group. Group 9, in particular, had two major polygon classes; pole size, moderately to well-stocked (SC2) lodgepole pine, and a mixture of subalpine fir, lodgepole pine and Engelmann spruce which was also in SC2. These two classes covered 44 percent of hectares in HT group 9. Douglas-fir or a mixture of Douglas-fir and ponderosa pine, in pole size to large-tree stands with broken, low-density canopies were also a relatively important classes in habitat type group 2, representing about one third of the hectares in this HT group.

Table 5.6: Major polygons in M332a by habitat type group, forest type and structure class.

HT Group	Forest Type	Structure Class	Hectares in Sample	% in sample	% of HT Group
9	LP	2	304	3.7	25
2	DF	4	293	3.6	16
2	DFPP	4	245	3.0	14
9	AFLPS	2	243	3.0	20
5	C	3	213	2.6	16

Cover types. Five cover types were about equally important in the 1975 sample of M332a (Table 5.7). The "alpine" cover type was slightly more common than Douglas-fir cover type or ponderosa pine mixtures. Grand fir or grand fir/cedar cover type was also fairly common on lower elevation sites and lodgepole pine cover types were as common on high elevation sites. Alpine cover type catches stands which fail to classify as any other type, and occur on subalpine fir "climax" habitat types. The forest types of these polygons are generally (72 percent of hectares) some combination that included subalpine fir, mountain hemlock or whitebark pine. The remainder are combinations of lodgepole pine and larch with Douglas-fir and/or grand fir.

In 1935, the "alpine" cover type was assigned mostly on the basis of the cover not qualifying as one of the other cover types on sites occurring at high elevation. There was no specified elevation cutoff for alpine cover. In Leiberg's 1899 report on the Priest River Reserve (Leiberg 1899), the alpine type was described as 28 percent whitebark pine and 70 percent subalpine fir.

The Priest River Reserve was the Priest River drainage, in what is now Priest River Ranger District of the Idaho Panhandle National Forests and a small part of the Colville Ranger District of the Wenatchee National Forest. He also reported small amounts of Engelmann spruce, Douglas-fir (as red fir), lodgepole pine, western white pine and western larch (as tamarack) in the alpine type. In his 1895 report (Leiberg 1897) on the Coeur d'Alene mountains (mostly the Coeur d'Alene National Forest of the Idaho Panhandle), he described the subalpine fir cover type occurring in nearly pure stands and the white bark pine type mixed with mountain hemlock (as Patton's hemlock). Leiberg devoted considerable text to discussion of the destruction of both the Priest River Reserve and the Coeur d'Alene mountain forests through intentional burning by mineral prospectors. Leiberg's surveys took place approximately 35 to 40 years before the 1935 forest surveys used the present analysis. Although his species descriptions are useful in characterizing the general species mixes within the various cover types, there were probably significant changes in composition, ages and structures of forests between Leiberg's surveys at the turn of the century and the 1935-era surveys.

In the "Bitterroot Forest Reserve" which is more relevant to ecosection M332a, Leiberg (1900) described the subalpine fir type as sharing site dominance with Engelmann spruce, whitebark pine and, sometimes, alpine hemlock and alpine larch (as Lyall larch). Although whitebark pine is described by Leiberg as present in the alpine forests, he also noted that the tree constituted "less than 1 percent of the forest growth in the reserve." Interestingly, he also noted that whitebark pine appeared to be "not holding its own, but is gradually being crowded out by alpine fir, lodgepole pine, and Engelmann spruce."

The Douglas-fir cover type and ponderosa pine mixed type were found mostly on warm and moderate to dry habitat types. These types constituted 80 percent of HT group 2, 54 percent of HT group 1, 38 percent of group 4, and 24 percent of group 5 in 1975. In the 1935-era survey, Douglas-fir cover type and ponderosa pine mixed type was assigned to only 36 percent of HT group 2, 26 percent of group 1, and 11 percent of group; ponderosa pine cover type (essentially pure pine) was much more common in HT groups 1 and 2, covering 51 percent and 45 percent, respectively. The greatest difference in the sample of HT group 4 was in the western larch/Douglas-fir cover type, which was assigned to 50 percent of hectares in the 1935 era and less than 1 percent in the 1975 era. In HT group 5, the amount of Douglas-fir and mixed ponderosa pine types remained nearly constant between 1935-era and 1975-era surveys, with 27 percent in the 1975 survey.

Table 5.7: Cover types of sample polygons in the 1935 and 1975 eras.

Description*	Code	% *1 1935	% *2 1975 Subsample	% *3 1975 All
White pine GE** 15%	1	7	0	0
Ponderosa pine GE 80%	2.8	14	4	4
Ponderosa pine GE 25%	2	8	14	18
Western larch and Douglas-fir GE 75% with larch GE 10%	3	9	1	1
Douglas-fir GE 60%	5	14	21	18
Engelmann spruce GE 50%	6	1	2	4
Lodgepole pine GE 50%	7	21	13	13
Western redcedar GE 50%	8	2	4	3
Western redcedar and grand fir GE 50% (at least one live C)	9	5	11	16
"Alpine"	11	10	27	19
Non-forested because of site factors limiting tree survival	19, 23, 17, 18	4	2	3
Non-forested because of tree harvests	13,14	0	0	0
Non-forested because of wildfires	15,16	2.5	0	0
Non-forest because of cultivation	21	0	0	0

* The cover types are listed in priority. Stands were assigned the first cover type for which they qualified. Percent compositions are by cubic foot volume in sawlog stands and live trees per acre in seedling to pole-size stands.

** GE = greater than or equal to.

*1 Percent of hectares in 1935-era sample.

*2 Percent of hectares from 1975-era survey in sample polygons also surveyed in the 1935 era.

*3 Percent of hectares from 1975-era survey in all sample polygons (includes some not surveyed in 1935).

Polygon Classes Based on Cover Type

With 135 polygon classes based on habitat type group/cover type/structure class, it was unusual for any one class to cover more than about 5 percent of the sample area in 1975. From a total of 35 classes in the 1975 sample, using the combination of cover type and structure class,

the top six classes covered nearly half of the area. Lodgepole pine and "alpine", both in structure class 2, covered 11 percent and 8 percent, of hectares, respectively. Douglas-fir cover type, and ponderosa pine mixed type in structure class 4 (large tree, broken canopy) were assigned to 9 and 7 percent. And grand fir/cedar in structure classes 3 and 4 covered 14 percent of hectares, combined.

There were 103 HT group/cover type/structure class polygon classes in the 1935 era. Of 28 combinations of cover type and structure class present in the 1935 sample, seven cover type/structure class combinations comprised half of the hectares. Lodgepole pine and "alpine," structure class 2, had been assigned to 14 percent and 7 percent, respectively. Non-forested sites, primarily as a result of wildfires, were found on 8 percent of hectares. Western larch/Douglas-fir and Douglas-fir, both in structure class 2, covered 7 percent, each. And ponderosa pine mixed cover type in a large-tree, open-canopy structure (SC4) was assigned to 7 percent of hectares.

Within habitat type groups, there were several significant changes in proportions of polygon classes from 1935 era to 1975 era. The greatest changes are seen in declining western larch/Douglas-fir and pure ponderosa pine types, and increases in subalpine fir and grand fir cover types with large-tree structure classes (Table 5.8). These changes may have caused significant losses or gains in habitat for associated plant and animal species.

Table 5.8: Changes in proportion of prevalent polygon classes in the 1935 and 1975 eras.

Polygon Class			Proportion Of HT Group	
HT Group	Cover Type	Structure Class	1935 era	1975 era
3	3	2	.40	.00
2	2.8	4	.35	.03
4	3	2	.32	.00
3	7	2	.32	.22
1	2.8	4	.31	.14
9	7	2	.29	.44
7	11	3	.04	.27
5	9	3	.21	.26
2	2	4	.20	.24
1	2	4	.14	.23
4	9	4	.00	.19
3	9	4	.00	.19

Trends in cover type. In the 1935-era survey, lodgepole pine, ponderosa pine, Douglas-fir and western larch were the most common cover types overall. Together they constituted 68 percent of hectares. By the 1975 era, subalpine fir had increased from only 10 percent to 27 percent of hectares. Grand fir more than doubled and Douglas-fir and western redcedar also increased significantly (Figure 5.1). During this same period western larch and ponderosa pine cover types declined dramatically, as did the small amount of western white pine present in 1935. Lodgepole pine also decrease greatly, although proportionately less than the other early seral species.

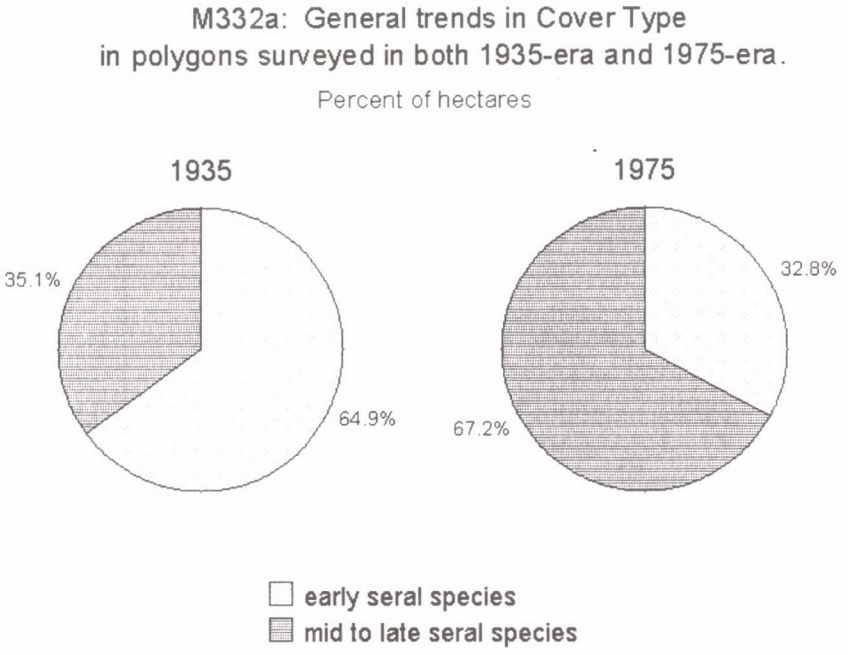

Figure 5.1: General trends in cover type, 1935 and 1975 eras.

The overall trends in cover type changes could be generalized into four categories:

1) Increases in the relative stocking of later seral (or climax) species. This was commonly a change from relatively pure ponderosa pine to a ponderosa pine/fir mixture or from Douglas-fir to western redcedar or grand fir.

2) Retention of similar relative stocking of early seral species. In this case, the species may change as long as the replacement is also an early seral species. For example, a change from ponderosa pine to lodgepole pine cover type or from western larch mixed with Douglas-fir to ponderosa pine mixed with fir.

3) No change in species composition, or at least not enough change to result in a change in the cover type class. This was seen primarily in mid to late seral species stands in which cover types are expected to be retained for extended periods (at least in excess of 40 years).

4) An increase in the relative stocking of earlier seral components compared to later seral components. This was typically a change from Douglas-fir to a pine type (ponderosa or lodgepole pine) or from mixed ponderosa pine type to relatively pure pine.

Not surprisingly, the dominant trend in cover type was an increase in later seral species composition (Figure 5.1). Nearly 3/4 of the sample area either followed this trend or began with a mid- to late-seral cover type that remained constant throughout the period. Most of the remaining polygons retained early seral components, with only 7 percent of hectares actually increasing in composition of pines or larch, or in a few cases, Douglas-fir (Table 5.9).

Table 5.9: Trends in cover types in M332a, 1935 era to 1975 era.

Trends in Cover Type in M332a	Proportion (ha.)
Increase later seral species composition	.52
Maintain early seral components	.20
Species composition stable (no change occurred)	.21
Increase proportion of early seral components	.07

Trends in structure classes. Among seven recognized types of structure trends, stable structures in which changes were not sufficient to result in a different structure class in 1975 era from that assigned in 1935 era were observed in a little more than one fourth of hectares (Table 5.10). This was typically seen in structure class 3 which remained structure class 3, or in structure class 2 on high elevation sites that are not expected to grow to diameters required to meet criteria for structure class 3. In this case, structure class 2 remaining structure class 2 is considered stable. The expected change from small trees to larger trees and denser stands was the next most common occurrence, seen in 17 percent of hectares.

Prevention of canopy closure was also seen in 17 percent of hectares. Here, the average tree size generally increased, but the stocking density became, or remained, low. This trend was nearly always the function of one or more of the pathogens and insects. Another significant function of pathogens and insects resulted in succession being suspended, with young, and small tree classes remaining so. Here, a stand often started in structure class 1 and ended in this class 40 years later.

Decreases in density moving polygons from SC 3 to 4 were fairly uncommon in the sample of M332a.

Table 5.10: Trends in structure classes in M332a, 1935 era to 1975 era.

Trends in Structure in M332a	Proportion (ha.)
Normal change to larger trees with nearly closed canopies	.17
Canopy closure prevented (low canopy density results)	.17
Largest trees die; move toward young, small tree classes	.18
Structure stable (no change occurred)	.27
Structure stalled in young, small tree class	.12
Large-tree structure; increase in canopy density	.08
Large-tree structure; decrease in canopy density	.02

The net result from these tends in structure class changes has been a shift toward more large-tree, closed-canopy stands (Figure 5.2). Most of the gains in this structure class was from pole size, moderate- to high-density stands and from large-tree stands that had net increases in tree volumes (Table 5.11). Structure classes 2 and 4 exchanged about an equal number of hectares: That is, about as many hectares in class 2 gained enough in diameter and tree volume to become class 4, as lost enough diameter and tree volume to move backward from class 4 to class 2. A remarkable 32 percent of hectares in structure class 1 in 1935 were still in this structure class 40 years later.

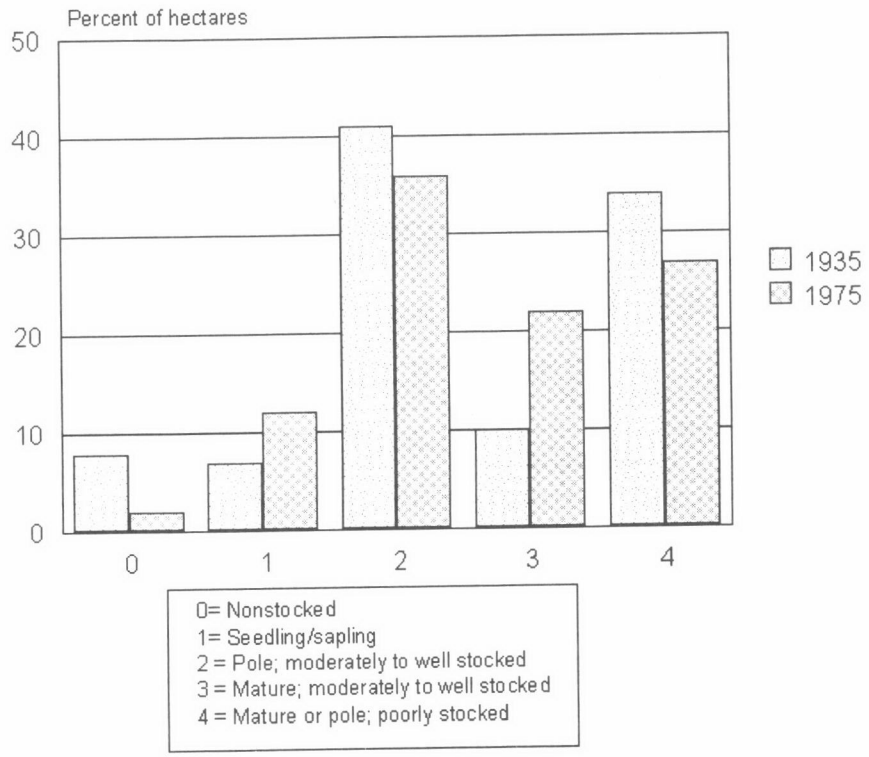

Figure 5.2: Structure-class distribution in the 1935 and 1975 eras.

Table 5.11: Distribution of structure classes in M332a sample polygons in 1935 era and structure classes into which they were classified 40 years later (shown as percent of hectares).

1935 Structure Class	Description	% 1935	1935 Ha.	1975 Structure Class	% 1975
0	Non-forested	8	479	0	17
				1	20
				2	23
				3	10
				4	30
1	Seedling/sapling	7	448	0	1
				1	32

				2	54
				3	1
				4	12
2	Pole; moderately to well-stocked	41	2,577	0	0
				1	6
				2	55
				3	18
				4	21
3	Large tree; well-stocked	10	646	0	0
				1	2
				2	6
				3	64
				4	28
4	Large tree; poorly to moderately stocked	34	2,165	0	1
				1	14
				2	22
				3	23
				4	41

ECOSECTION M333D

Sample Location

Referred to as the Bitterroot Mountains Ecosection, this ecosection covers most of the northern half of north Idaho and west-central Montana (see Figure 2.1). Parts of the Idaho Panhandle, Clearwater, Lolo and Kootenai National Forests were sampled within ecosection M333d (Table 5.12).

Table 5.12: M333d: National Forest land included in the sample of M333d.

National Forest	Hectares in Sample	Percent of 1975-era Sample
Idaho Panhandle NF's	13,613.5	59.6
Clearwater NF	3,798.4	16.6
Lolo NF	3,706.2	16.2
Kootenai NF	1,714.2	7.5

Habitat Types

Of the 38 habitat types represented in the sample polygons, 9 were common. *Tsuga heterophylla/Clintonia uniflora* (28.8 percent of the total sample area) , *Thuja plicata/C. uniflora* (16.7 percent) and *Abies grandis/ C. uniflora* (10.9 percent) had been assigned to over half of the total hectares. Both *T. heterophylla/C. uniflora* and *T. plicata/C. uniflora* are in habitat type group 5 (moderately cool and moist). *Abies grandis/C. uniflora* is in habitat type group 4 (moderately warm and moist). Habitat type group 5, which is represented by 45.5 percent of the total hectares in the sample, is described as sites on which very high basal area can be achieved (Table 5.13). Habitat type *Tsuga mertensiana/Menziesia ferruginea* (6.8 percent of sample) was the most common type in group 7, described as cool and moist sites. Most important in group 9 were *Abies lasiocarpa/Xerophyllum tenax* (7 percent) and *T. mertensiana/Xerophyllum tenax* (5.8 percent). Habitat type groups which were insufficiently represented to allow characterization of the pathogen and insect functions included; 1, 6, 8 and 15. In group 10, only *A. lasiocarpa/Luzula hitchcockii* habitat type was represented. In group 11, only *Pinus albicaulis-A. lasiocarpa* habitat types were represented. Although groups 10 and 11 were not sufficiently represented to characterize the groups, the habitat types *A. lasiocarpa/L. hitchcockii* and *P. albicaulis-A. lasiocarpa* were probably sampled adequately to characterize pathogen and insect functions in major cover types.

Table 5.13: Habitat type groups represented in the 22, 832 hectares of sample polygons for ecosection M333d in the 1975-era survey.

HT Group	Characteristics	Hectares 1975-era	%[1] 1975 Sample
1	Warm/dry	87	0.4
2	Moderately warm/dry	2320	9.9
3	Moderately warm/moderately dry	683	3.2
4	Moderately warm/moist	2428	10.9
5	Moderately cool/moist	10514	45.5
6	Moderately cool/wet	4	0
7	Cool/moist	3559	15.6
8	Cool/Wet	5	0
9	Cool/moderately dry	2889	13.1
10	Cold/moderately dry	189	0.8
11	Cold	104	0.4
15	Grassland/steppe	56	0.2

[1] 1 percent of hectares in 1975-era sample

Cover Types in 1975-era Sample

The definitions used in the 1935-era survey for cover type were skewed in favor of western white pine, ponderosa pine, and, to some extent, western larch. Even so, the proportions of ponderosa pine and larch/Douglas-fir type in the 1975 era were very low, with a total of only 4 percent in ponderosa pine cover types and 3 percent in the western larch/Douglas-fir mixed type (Table 5.14). White pine cover type was among the most common, second only to "alpine" but it was assigned to many polygons which did not have western white pine assigned as a component of the forest type.

Table 5.14: M333d: Proportion by cover type class of 22,832.3 hectares in the 1975-era sample.

Description*	Code	Hectares 1975-era	%
White pine GE** 15%	1	3786.4	16.6
Ponderosa pine GE 80%	2.8	126.1	0.1
Ponderosa pine GE 25%	2	671.6	2.9
Western larch and Douglas-fir GE 75% with larch GE 10%	3	689.4	3.0
Western hemlock and grand fir GE 50% (at least one live WH)	4	2468.9	10.8
Douglas-fir GE 60%	5	2365.5	10.4
Engelmann spruce GE 50%	6	255.3	1.1
Lodgepole pine GE 50%	7	2763.3	12.1
Western redcedar GE 50%	8	361.6	1.6
Western redcedar and grand fir GE 50% (at least one live C)	9	3262.9	14.3
"Alpine"	11	5575.0	24.4
Non-forested	19	506.3	2.2
Non-forested because of tree harvests	13,14	274.0	1.2

* The cover types are listed in priority. Stands were assigned the first cover type for which they qualified. Percent compositions are by cubic foot volume in sawlog stands and live trees per acre in seedling to pole-size stands.

** GE = greater than or equal to

Of the 3786.4 hectares that were cover type code 1 (white pine), only 29 percent were assigned forest types that included western white pine (Table 5.15). Other than western white pine, the most prevalent components of the forest types corresponding to cover type code 1 were western hemlock, grand fir, Douglas-fir, western redcedar, and subalpine fir. A few also had some western larch, lodgepole pine, or Engelmann spruce.

Table 5.15: Forest type components prevalent in polygons assigned cover type Code 1, ecosection M333d, 1975 era.

Forest Type Component	Proportion
Western white pine in any combination (none were more than 80 percent western white pine)	.29
Western hemlock in mix without white pine	.37
Cedar in mix; no white pine or western hemlock	.08
Subalpine fir in mix; no white pine, western hemlock or western redcedar	.02
Grand fir in mix; no white pine, western hemlock, western redcedar or subalpine fir	.15
Douglas-fir in mix; no white pine, western hemlock, western redcedar, subalpine fir or grand fir.	.04

While only 7.8 percent of the cover type code 3 was also coded as western larch (L) forest type, 63 percent of the hectares in cover type 3 were assigned forest types with L as one of two or three species codes (Table 5.16). In contrast, 66 percent of the hectares assigned cover type code 5, Douglas-fir, were also code Douglas-fir (DF) forest type and 94 percent had DF as a component in the two or three species code. Similarly, 42 percent of those coded cover type 7, lodgepole pine, were coded lodgepole pine (LP) forest type and 95 percent had LP as a component in the two or three species code.

Table 5.16: Ecosection M333d, 1975-era forest types of polygons assigned cover type Code 3.

Forest Type	Proportion
DF	31.4
DFL	17.4
DFGFL	13.9
C DFL	8.1
L	7.8
DFGF	4.8
GFL	3.7

C DFWH	3.5
AFDFL	3.4
GFL WH	2.0
Other	4.0

Forest Types in the 1975-era Sample

Because of the great number of combinations of species that may occur in ecosection M333d, there were too many forest types to provide a meaningful grouping of polygons. Few of the types were represented in more than 1 percent of the sample hectares. There were 125 unique forest types assigned. The best-represented forest types are presented in Table 5.17.

Table 5.17: Major forest types in 22,823 hectare sample of M333d.

Forest Type	Hectares in Sample	Percent of Sample
DF	2269	10.3
LP	1265	5.7
DFGF	1168	5.3
GF	1122	5.1
GFWH	1077	4.9
DFGFWH	1046	4.7

Although western white pine was represented as a significant component (as part of forest type) on 1,238 hectares (5.6 percent), it was present as at least 66 percent of the basal area on only 3 hectares of the sample.

Structure Classes in the 1975-era Sample

Relatively little of the sample area was in a non-forested structure class such as shrubs or grass (Table 5.18). Pole-size stands with moderate to good density were most common, followed by sawlog-size stands with good density. Sawlog-size stands (classified as structure classes 3 and 4) were not commonly produced on the cooler, drier sites typically dominated by subalpine fir and lodgepole pine. As expected, the majority of these structure classes was seen on the most productive habitat types in groups 4 and 5. Structure class 4, representing mostly mature stands with broken canopies and relatively poor density, was also common in habitat type groups 4 and 5. These also tended to have fairly high index values for some of the pathogens and insects. The low stocking was probably the result of pathogens and insects killing mature trees and/or killing a large percentage of trees throughout the process of stand development.

Table 5.18: Distribution of structure classes in 22,823 hectare sample of M333d in 1975-era survey.

Structure Class	Description	Hectares in Sample	Percent of Sample
0	Non-forested	506	2.2
1	Seedling/sapling	3303	14.5
2	Pole; moderately to well-stocked	9439	41.3
3	Large tree; well-stocked	5209	22.8
4	Large tree; poorly to moderately-stocked	4375	19.2

Age related to structure classes. Stand age was calculated as basal area- weighted tree ages which were then weighted by polygon hectares. The result is a general indication of the representative age of structure classes (Table 5.19). Polygons with structure class 3 were consistently older than those with structure class 4, on average, within habitat type groups as well.

Table 5.19: Relationship of average age structure classes and proportion of structure classes 3 and 4 by bd.ft./acre live timber volume classes.

		Proportion of SC in each bd.ft./acre class (*1000 bd.ft.)					
Structure Class	Age	0-10*	10-20	20-30	30-40	40-50	50+
0	45**	1.00					
1	22	1.00					
2	59	0.70	0.24	0.06			
3	113	0.00	0.04	0.46	0.27	0.20	0.03
4	89	0.38	0.62	0.00	0.00	0.00	0.00

*The high weighted average ages in structure class 0 results from the presence of very few large, old trees in some polygons with too little total basal area or trees per hectare to qualify as "forested."

Timber volume related to structure classes. Within the habitat types and structure classes that were expected to have the greatest timber volumes, habitat type groups 2, 3, 4, and 5 and structure classes 3 and 4, few stands had boardfoot (bd.ft.) volumes which the sites are considered capable of producing. Only 23 percent of the sample area M332a in habitat type groups 2, 3, 4, and 5 with structure class 3 and had in excess of 40,000 bd.ft./acre. Stands in these

habitat type groups in structure class 4 did not exceed 20,000 bd.ft./acre despite averaging 89 years of age.

Polygon Classes Based on Forest Type

The combinations of habitat type groups, forest types and structure classes represented in the sample resulted in 443 unique polygon classes in M333d. Most classes had very few hectares in the sample, but a few were fairly well-represented (Table 5.20). Not surprisingly, Douglas-fir and grand fir components were prominent in the common polygon classes.

Table 5.20: The top 10 polygon classes each represented less than 3 percent of hectares in the 1975-era sample of M333d.

HT Group	Forest Type	Structure Class	Hectares in Sample	Percent in Sample	Percent in HT Group
2	DF	2	579	2.6	26.3
5	WH	3	576	2.6	5.7
5	GFWH	4	438	2.0	4.4
5	GFWH	3	419	1.9	4.2
2	DF	4	361	1.6	16.4
4	DFGF	4	355	1.6	14.8
5	C DFGF	2	345	1.6	3.4
5	C DFGF	3	326	1.5	3.2
5	DFGFWH	3	315	1.4	3.1
5	C	3	289	1.3	2.9

There was little uniformity in the sample. The largest polygon classes were each less than 3 percent of the total sample hectares and they generally also constituted a fairly small part of the hectares in the habitat type group to which it belonged. Notable exceptions were HT group 2, DF, SC 2 and 4 which in combination comprised 42.7 percent of the hectares in HT group 2. Similarly, HT group 4, DFGF, SC 4 and HT group 4, GF, SC 4 comprised 25.6 percent of hectares in HT group 4.

Cover Types in the 1935-era Sample.

The cover type classification system used in the 1935-era survey was strongly skewed in favor of species of economic interest such as western white pine, ponderosa pine, and western redcedar. A few of the subcompartments sampled in the 1975-era survey were not covered in the 1935-era maps. Of 22,065 hectares sampled in the 1935 era, 34.7 percent were identified as

western white pine or mixtures containing at least 15 percent western white pine (Table 5.21). Western larch-Douglas-fir cover type was identified on 16.3 percent of hectares. For these, 75 percent by volume (TPA for small trees) composition of Douglas-fir and western larch was required with at least 10 percent western larch. Although ponderosa pine was given similar classification advantages, only 5.5 percent of hectares were identified as ponderosa pine cover types (at least 25 percent ponderosa pine). Cedar cover type required a 50 percent composition of cedar or cedar and grand fir combined, but was identified on only .2 percent (cedar greater than 50 percent) and .5 percent (cedar and grand fir greater than 50 percent) of hectares in the sample.

Table 5.21: M333d: cover types of sample polygons in the 1935 era compared to the 1975 era.

Description*	Code	%1 1935-era	%2 1975-era
White pine GE** 15%	1	34.7	17.1
Ponderosa pine GE 80%	2.8	1.3	0.7
Ponderosa pine GE 25%	2	4.2	3.1
Western larch and Douglas-fir GE 75% with larch GE 10%	3	16.3	2.8
Western hemlock and grand fir GE 50% (at least one live WH)	4	2.0	11.0
Douglas-fir GE 60%	5	6.4	10.7
Engelmann spruce GE 50%	6	0.9	1.1
Lodgepole pine GE 50%	7	7.5	12.4
Western redcedar GE 50%	8	0.2	1.6
Western redcedar and grand fir GE 50% (at least one live C)	9	0.5	3.1
"Alpine"	11	8.9	24.8
Non-forested because of site factors limiting tree survival	19, 23	0.6	0.6
Non-forested because of tree harvests	13, 14	0.5	1.2
Non-forested because of wildfires	15, 16	16.0	0.0
Non-forested because of cultivation	21	0.1	0.0

* The cover types are listed in order of priority. Stands were assigned the first cover type for which they qualified. Percent compositions are by cubic foot volume in sawlog stands and live trees per acre in seedling to pole-size stands.

** GE = greater than or equal to

1 Percent of hectares in 1935-era sample

2 Percent of hectares in sample polygons from 1975-era survey that had also been surveyed in the 1935 era.

Structure Classes in the 1935-era Sample

Large tree structures with open canopy conditions were common in the 1935-era sample for M333d (Table 5.22). This structure class was most commonly seen in white pine and western larch cover types and in "alpine" cover type on habitat type group 7 sites. With a relatively large proportion of the area coded as non-forested due to wildfires (codes 15 and 16 in Table 5.21), it is likely that fires also accounted for much of the open canopy conditions seen in the structure class 4 stands. Seedling and sapling structure class was second most common in the 1935-era sample. This condition probably also resulted largely from recent burns. Structure class 3, representing large tree structures with sites nearly completely occupied by large trees was relatively uncommon in the 1935-era sample, making up only 7.2 percent of the area.

Table 5.22. Distribution of structure classes in M333d sample in the 1935 and 1975 eras.

Structure Class	Description	Hectares in 1935 Sample	% * 1935	Hectares in 1975 Subsample	% ** 1975
0	Non-forested	3758	17.1	394	1.8
1	Seedling/sapling	5646	26.7	3248	14.7
2	Pole; moderately to well-stocked	3969	18.0	9303	42.1
3	Large tree; well-stocked	1588	7.2	5022	22.7
4	Large tree; poorly to moderately-stocked	7042	32.0	4139	18.7

* Percent of hectares in 1935-era sample

** Percent of hectares from 1975-era survey for the subsample surveyed in both 1935 and 1975 eras.

How Polygon Vegetation Changed in 40 Years

The overall trend in cover type was toward mid- to late-seral species such as subalpine fir, grand fir, western hemlock, Douglas-fir, and western redcedar (Figure 5.5). Western white pine and western larch cover types were lost in great quantities, but there was a small increase in lodgepole pine cover type. The most striking trend in structure classes was a doubling of structure class 2; pole size, moderately to well-stocked stands (Figure 5.6). Structure class 3 also increased considerably, while structure classes 0, 1, and 4 all declined.

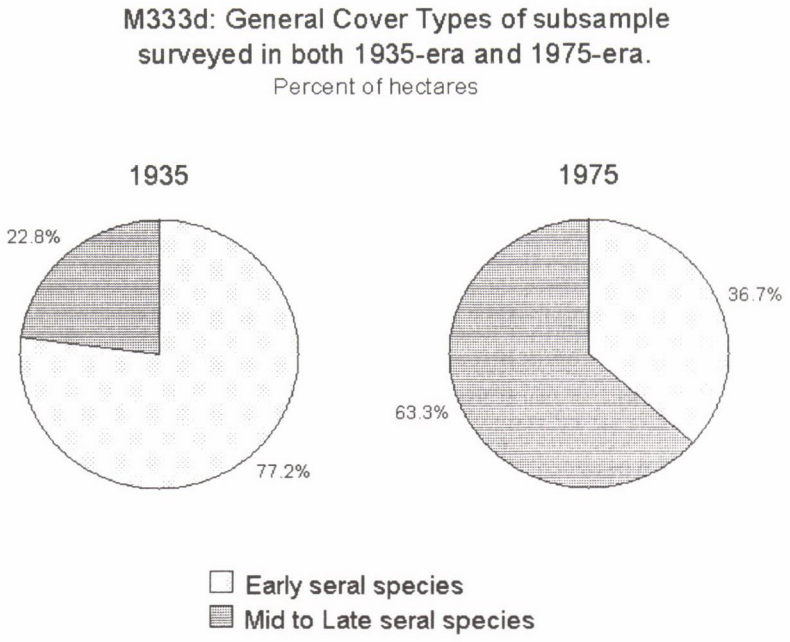

Figure 5.5: General cover types in M333d in 1935 era and 1975 era.

Figure 5.6: Structure class distribution in M333d in the 1935 and 1975 eras.

The majority of hectares in the initial structure classes representing young stand structures progressed in ways expected based on stands maturing and ingrowth increasing stand closure (Table 5.23). For example, the non-forested sites generally (80 percent) progressed to seedling, sapling or moderately- to well-stocked pole stands. Likewise, seedling and sapling stands mostly (69 percent) progressed to moderately- to well-stocked pole stands. Stands which were in moderately- to well-stocked pole stands initially were somewhat less uniform in their progression. While 44 percent remained in the same class, about a half the of hectares progressed to larger tree size classes with equal proportions becoming well-stocked (structure class 3) and moderately to poorly stocked (structure class 4).

Structure class 3 would generally be expected to remain in this class in the absence of large disturbances and half of the hectares in this class did remain so, but only 44 percent of these retained the same cover type (Table 5.23). This is probably largely because 93 percent of the structure class 3 hectares in the 1935 sample of M333d were cover type 1, western white pine. Of the hectares with western white pine cover type which were classified as structure class 3 in both 1935 and 1975, 47 percent also retained the white pine cover type. With white pine cover type only requiring that at least 15 percent of the cubic foot volume is white pine, there could have been considerable loss of white pine composition in the stands without a change in cover type.

Structure class 4, represented by stands with an overall large tree size class but with low to moderate stocking, was a very common class in 1935 (Table 5.23). Stands in this initial class were only slightly more likely to progress to higher stocking (structure class 3) than to remain in the same class, or fall below the minimum requirement for volume of large diameter trees (moving to structure class 2). Fifteen percent of hectares changed from structure class 4 to class 1, seedlings and saplings.

Table 5.23: Changes in structure class from the 1935-era to 1975-era surveys for the 22,002.9-hectare subsample of M333d surveyed in both periods.

1935 era		1975 era	Transition
Structure Class	**Hectares**	**Structure Class**	**Proportion**
0	3,758	0	.05
		1	.35
		2	.45
		3	.02
		4	.12
1	5,646	0	.02
		1	.07
		2	.69

		3	.07
		4	.15
2	3,969	0	.00
		1	.06
		2	.44
		3	.25
		4	.24
3	1,588	1	.13
		2	.17
		3	.51
		4	.18
4	7,042	0	.01
		1	.15
		2	.23
		3	.39
		4	.22

All of the 11 cover types represented in the 1935-era sample also were present in the sample in 1975-era. However, relatively few polygons (25.3 percent of hectares) had the same cover type in both the 1935 era and the 1975 era. Nearly all polygons had changed to a new polygon class, with only 7.1 percent of hectares remaining the same polygon class after 40 years.

The cover types, with only 11 classes represented, are relatively broad classes compared to forest types which were represented by 125 classes represented by the same polygons. But the rate of change was similar for both classification systems. Classification using habitat type group/cover type/structure class resulted in 139 classes represented by 1935-era polygons and 160 classes represented by 1975-era polygons. Using habitat type/probable forest type/structure class resulted in approximately 275 probable classes for 1935-era polygon data and 392 classes in the 1975-era polygons. Even with this large difference in numbers of classes, the rate of change in polygons classified using habitat type group/cover type/structure class was 92.9 percent of hectares compared to 95 percent for the same polygons classified using forest type in the place of cover type.

In the 1935 era, the largest cover type classes were western white pine (code 1), 33.6 percent of total hectares, and non-forested (codes 13,14,15,16,19,21, or 23), 22.4 percent of total hectares. Nearly 80 percent of the non-forested hectares had been coded 15 or 16; burned before, or after, 1925. Only 94 hectares, less than 1 percent, was non-forested because of having been harvested. In the 1975-era resurvey, western white pine cover type was found on only 18 percent of the total sample hectares, and none were non-forested because of burning or harvest. Two percent were non-forested in the 1975 era, mostly because of poor site quality (nonstockable). Of the 19,846 hectares surveyed in both 1935 and 1975 eras, 38 percent were assigned pine or larch (fir and larch) cover types in 1975-era. These cover types came largely from western white pine cover type in the 1935 era, (39 percent), or from non-forested because of fires (16 percent), or from other pine or larch/fir cover types (33 percent). As expected, only a small proportion (7 percent) of the 1975-era pine or larch/fir cover type was found in polygons which had more shade-tolerant cover types in the 1935 era. Most of this had been Douglas-fir cover type (code 5); 6 of the 7 percent derived from tolerant cover types. These were all polygons with severe root disease.

Although a third (33 percent) of the non-forested, burned hectares in the 1935 era became pine or larch/fir forest types (in the 1975 era), all six of the polygons which had been non-forested because of harvest were in grand fir, western hemlock or Douglas-fir cover type classes in 1975-era. The sample of harvested polygons was very small, so these results could not be considered statistically significant.

Cover types that tended to remain the same were: subalpine fir, 86 percent remaining subalpine fir; and lodgepole pine, 61 percent remaining lodgepole pine. The next highest retention rate was 36 percent for both grand fir and western white pine. With the cover type definition so strongly in favor of western white pine cover type (requiring only 20 percent composition), it is not surprising that so many polygons retained a western white pine cover type even though the proportion of white pine undoubtedly declined significantly (this is indicated also in that only 7 percent of 1975-era forest types containing western white pine). However, the pine/fir cover type (code 2) should have had a similar advantage but had only a 20 percent retention rate. Ponderosa pine was found in only 4 percent of 1975-era cover types of the 19,846 hectares for which we had survey data in both 1935 and 1975 eras.

The majority of 1935-era western white pine cover type in our sample was in habitat type group 5, the warm, moist group representing most western redcedar and western hemlock habitat types. Of 6,672 hectares of western white pine cover type, 4,900 (73.4 percent) occurred in this habitat type group. Habitat type groups 4, 7 and 9 were also important groups for western white pine cover type. Structure class 1 was most common within the western white pine cover type class in the 1935 era, making up 40 percent of the cover type. Structure class 4 was assigned to 31 percent of the type. Surprisingly, only 18 percent of the western white pine cover type was assigned structure class 3. This indicates that only 18 percent of this type, the majority of which was found on the most productive habitat types in M333d, had at least 20,000 boardfoot volume per acre. The most common changes in cover type from the hectares which were western white pine cover type in the 1935 era were to subalpine fir (code 11), 19 percent, western hemlock/grand fir (code 4), 18 percent, and grand fir (code 9), 12 percent. In the 1975 era, 79 percent of the white pine type was found in habitat type group 5 and most (67 percent) of it was found in polygons which were also western white pine cover type in the 1935 era.

General Trends in Cover Types and Structure Classes from the 1935 Era to the 1975 Era

The types of cover type changes were generalized into four categories:

1) Increases in the relative stocking of later seral (or climax) species. This was commonly a change from relatively pure western white pine to a grand fir/cedar mixture or from Douglas-fir to western hemlock or grand fir.
2) Retention of similar relative stocking of early seral species. In this case, the species may change as long as the replacement is also an early seral species. For example, a change from western white pine to lodgepole pine cover type or from western larch mixed with Douglas-fir to lodgepole pine mixed with fir.
3) No change in species composition, or at least not enough change to result in a change in the cover type class. This was seen primarily in mid to late seral species stands in which cover types are expected to be retained for extended periods (at least in excess of 40 years).
4) An increase in the relative stocking of earlier seral components compared to later seral components. This was typically a change from Douglas-fir to a pine type (western white pine or lodgepole pine) or from "alpine" to lodgepole pine.

The most important cover type change occurring during this 40-year period was the increase in the later seral species composition overall (Figure 5.5). This type of change occurred on 70 percent of hectares in the sample (Table 5.24). Not only is this consistent with uninterrupted vegetation succession but it is also one of the most prevalent functions of the pathogens and insects investigated in this analysis.

The early seral components of stands (mostly pines and larch) underwent a dramatic decline in importance over the period. In most cases where the species composition was maintained, it was a result of the direct effects of an insect or pathogen which acted to kill or reduce growth of the later seral species (usually Douglas-fir or true firs) on the site, thereby favoring the continued survival of the earlier seral species.

Table 5.24: Trends in cover types in M333d, 1935 era to 1975 era.

Trends in Cover Type in M333d	Proportion of Hectares
Increase later seral species composition	.70
Maintain early seral component(s)	.22
Species composition stable (no change occurred)	.05
Increase proportion of early seral components	.03

Succession was suspended or stalled in early structural stages such as seedlings and saplings, or retrogressed as in moving from large trees with closed canopies toward smaller tree structures on about a third of hectares (Table 5.25). Of these, 36 percent increased or maintained their early seral species composition, 62 percent moved toward later seral species composition, and only the remaining 2 percent maintained a similar species composition.

About 17 percent of hectares underwent transitions in which canopy closure was prevented (Table 5.25), thereby moving directly to a structure class 4 (large trees with open canopy). Thirteen percent increased or maintained early seral tree species compositions while either remaining in a large-tree, closed-canopy class or undergoing a normal type of change in structure, such as from seedling/sapling to pole-size or large trees with closed canopies. Nearly 7 percent of hectares increased in density while either increasing or maintaining early seral forest types. The remaining 1 percent changed from large tree, closed canopy structures to large tree, open canopy structures.

Table 5.25: Trends in structure classes in M333d, 1935 era to 1975 era.

Trends in Structure in M333d	Proportion of Hectares
Normal change to larger trees with nearly closed canopies	.32
Structure stalled in young, small tree class	.20
Canopy closure prevented (low canopy density results	.17
Large-tree structure; increase in canopy density	.13
Largest trees die; move toward young, small tree classes	.12
Structure stable (no change occurred)	.05
Large-tree structure; decrease in canopy density	.01

The most common type of transition that occurred in the M333d sample was toward an increase in later seral species compositions while increasing tree size and density. A total of 33 percent of hectares underwent this type of transition. Pathogens and/or insects influenced these transitions on 66 percent of the hectares in this group despite the appearance of a fairly "normal" successional pathway. The most common influence of pathogens and insects in these transitions was pushing the species composition toward later seral tree species by killing early seral tree species.

SECTION 6: RESULTS
Part 2: Succession Trends

Most of the changes in forest conditions in our sample from the 1935 era to the 1975 era were strongly influenced by pathogens and insects. In ecosection M332a, nearly 85 percent of transitions were considered to have been largely functions of pathogens and insects (Figure 6.1). Similarly, 80 percent of transitions in ecosection M333d were pathogen and/or insect controlled. In M332a, there were 27 general types of succession functions observed in polygons with high probable effect from insects and pathogens. Of these, the most common type of function in ecosection M332a was to maintain early seral species on the sites while the suspending the structure in small, young tree structure classes (classes 1 or 2). This was seen on 20 percent of hectares (Figure 6.2). In M333d, of 28 general types of functions in stands with high probable effect from pathogens and insects, the most common was to move the species composition toward mid- to late-seral species while preventing canopy closure. This was seen on 22 percent of hectares in M333d.

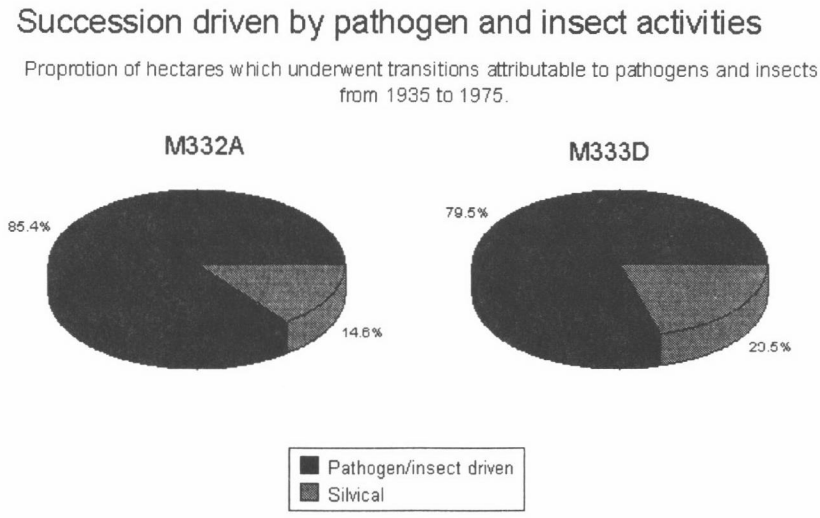

Figure 6.1: Percentages of pathogen and insect activity-driven succession.

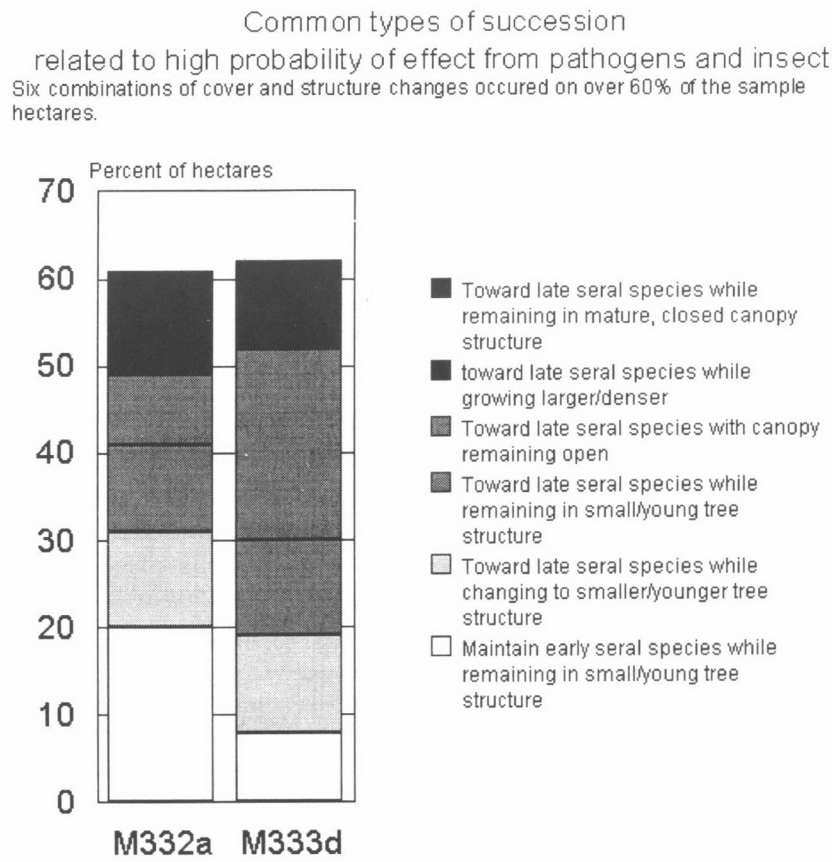
Common types of succession
related to high probability of effect from pathogens and insects
Six combinations of cover and structure changes occured on over 60% of the sample hectares.
Percent of hectares
70
60
50
40
30
20
10
0
M332a
M333d
Toward late seral species while remaining in mature, closed canopy structure
toward late seral species while growing larger/denser
Toward late seral species with canopy remaining open
Toward late seral species while remaining in small/young tree structure
Toward late seral species while changing to smaller/younger tree structure
Maintain early seral species while remaining in small/young tree structure

Figure 6.2: Common types of succession associated with pathogen and insect effects.

Among the polygons with high probable influence by insects and pathogens, they effectively suspended succession in small-tree structure classes or caused changes from large-tree to small-tree structures on 46 percent of hectares in M332a and 32 percent in M333d (Figure 6.3). This role was most evident on the most productive habitat types. Also during this 40-year interval, nearly 20 percent of hectares in M332a and 30 percent of M333d grew to large average diameters and relatively closed canopies. The net result of high probable effect of insects and pathogens was a nearly constant proportion of mature stands in both ecosections (Figure 6.4). Canopy closure increased somewhat in both ecosections, although this trend was more pronounced in M333d. The proportion of moderately to well-stocked pole stands decreased somewhat in M332a while seedling/sapling stand proportions increased. In M333d, pole-size stands increased in proportion while seedling/sapling stands remained about constant. The proportion of non-forested hectares in M333d was greatly diminished from the 1935 era to the 1975 era.

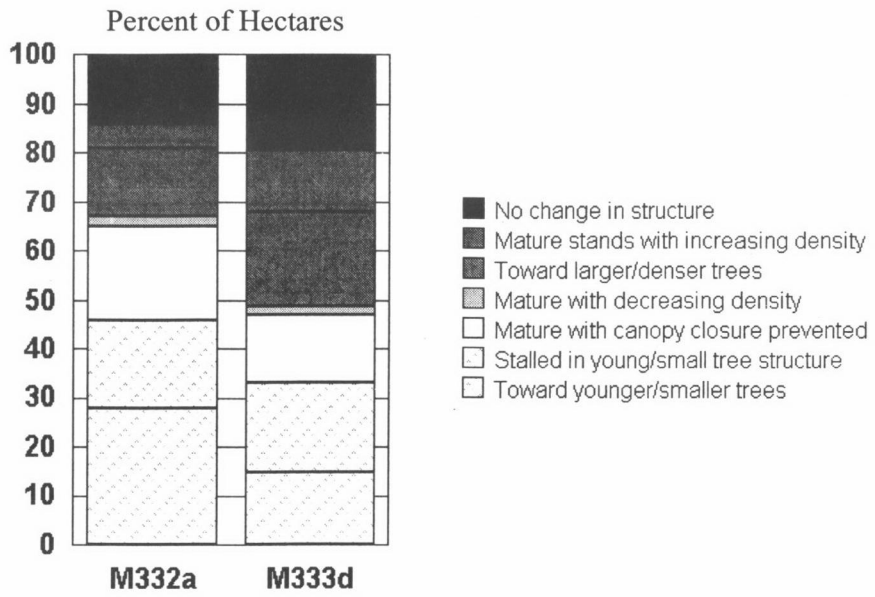

Figure 6.3: Structure changes in polygons with high pathogen and insect influence probabilities, 1935 era to 1975 era.

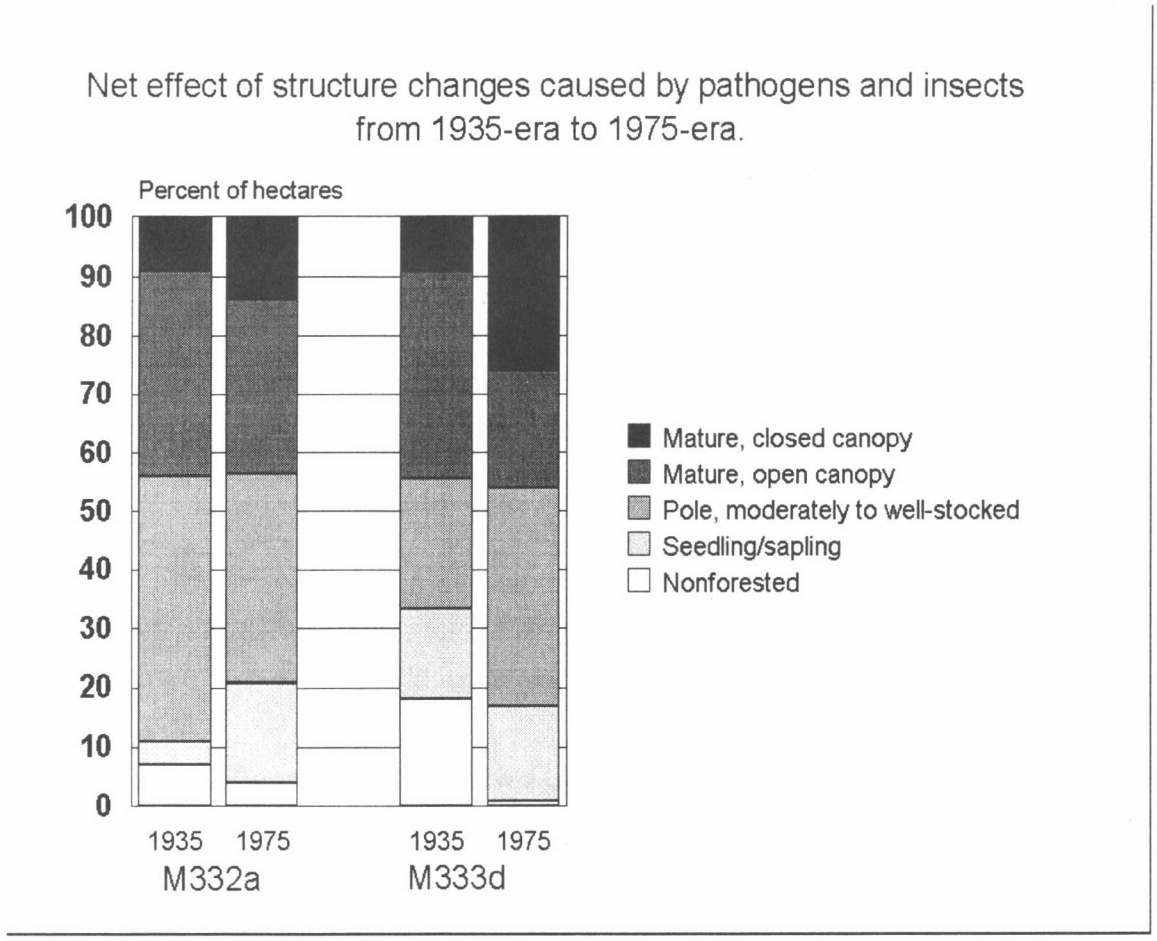

Figure 6.4: Net effect of structure changes by pathogens and insects.

Similar to polygons with little or no influence from pathogens and insects, the cover types trended strongly toward mid or late seral species compositions in both ecosections (Figure 6.5). In M333d, there was somewhat more tendency to retain early seral species, with 30 percent of hectares fitting this function type. This figure is somewhat elevated by the western white pine cover type requiring only 15 percent white pine composition so that even stands which have had heavy losses of western white pine may classify as white pine cover type. The net outcome of these high-probability functions in M332a (Figure 6.6) was a dramatic decline in lodgepole pine and western larch cover types with a corresponding increase in grand fir and subalpine fir types. In M333d (Figure 6.7), the major trends were away from non-forested, western white pine and western larch cover types and toward grand fir, subalpine fir and western hemlock types.

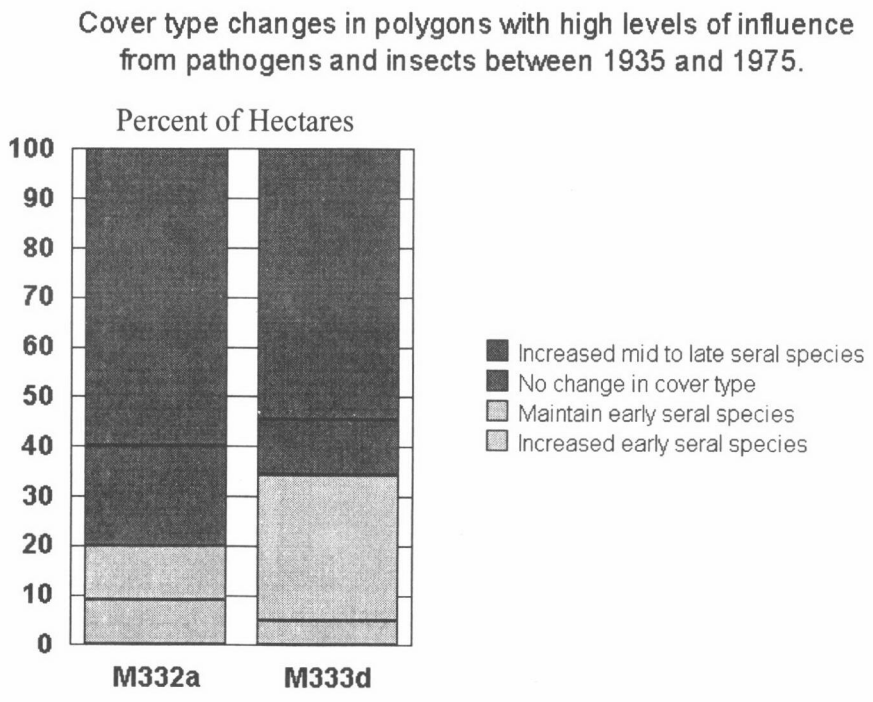

Figure 6.5: Cover type changes, 1935 era to 1975 era.

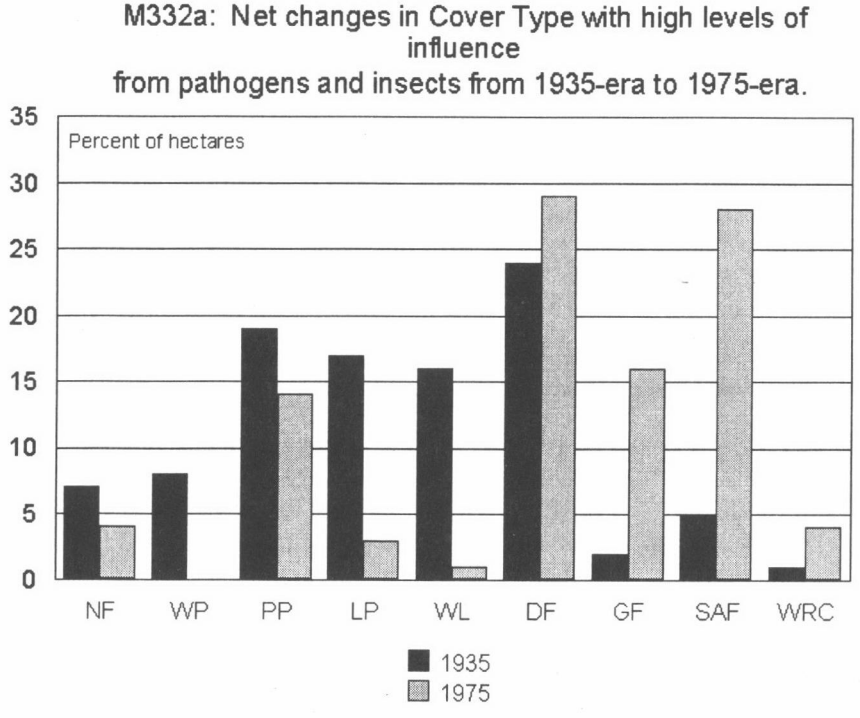

Figure 6.6: Net changes in cover type in M332a, 1935 era to 1975 era.

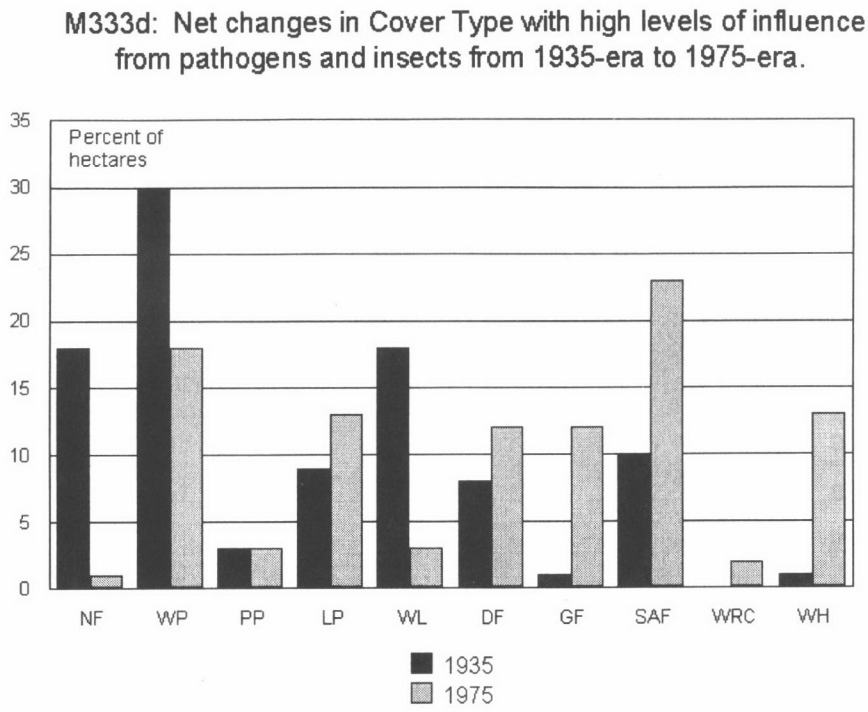

Figure 6.7: Net changes in cover type in M333d, 1935 era to 1975 era.

A high percentage (62 percent in M332a and 58 percent in M333d) of pathways were identified as likely unique to those produced by pathogens and insects. As such, they represent some of the important ways in which pathogens and insects maintain ecological diversity. Stalled or suspended succession is a good example of this type of pathway: in a 40-year time step, the polygons are seen to have remained in, or returned to a seedling/sapling class. Changes from large tree, closed-canopy conditions to those with smaller trees and/or broken-canopy conditions were usually associated with significant pathogen or insect activities. In this chapter, we look first at the succession influences of individual pathogens and insects, and then the successional influences of significant combinations of pathogens and insects are examined. In many cases, the outcomes produced by combinations of pathogens and insects are different from those produced by either agent acting alone.

WHITE PINE BLISTER RUST SUCCESSION FUNCTIONS

By John Schwandt

Introduction

White pine blister rust has had a very large impact on the forests in the inland west since its introduction in the early 1900s. Although blister rust has a complex life cycle that requires two hosts, this exotic disease found an abundance of highly susceptible hosts plus a very favorable climate in the Northwest, and quickly spread throughout the range of white pine. Blister rust spores from *Ribes* plants infect white pine through needles. The fungus then grows

into branches and down the branches to the main stem, where it girdles the tree and causes its death.

Prior to the arrival of white pine blister rust, white pines were common on all but the driest Douglas-fir and ponderosa pine habitat types. Western white pine was especially abundant in riparian areas, but was an integral part of subalpine forests as well. At higher elevations and colder harsher climates, it gives way to whitebark or limber pines, which are also highly susceptible to white pine blister rust.

White pine blister rust is actually considered to be of Asiatic origin, but had become well established throughout most of Europe by 1900, where eastern white pine from the US was widely planted for reforestation purposes (Mielke 1943, Moir 1924, Spaulding 1922). Millions of eastern white pine seedlings were grown in Europe and many shipments of infected seedlings from one nursery in Germany were made to over 200 localities in eastern North America between 1900 and 1910 to meet an increased demand for seedlings which the local nurseries were unable to meet. By 1909, the disease was found in seven eastern states and became widely distributed throughout the Northeast, upper Midwest, and eastern Canada in a relatively short time.

White pine blister rust wasn't discovered in the west until 1921, when it was found on black currant near Vancouver, British Columbia. Intense surveys that followed found it to be widely distributed on western white pine and ribes in British Columbia and primarily on ribes in Washington west of the Cascade Mountains. A diligent search of records traced it back to a single shipment of infected eastern white pine seedlings that had been raised in Ussy, France, and then shipped to a nursery near Vancouver, British Columbia, in 1910 (Mielke 1943, Eastham 1922).

Blister rust in western white pine (*Pinus monticola*)

By the mid-1930s, white pine blister rust was well established throughout much of the Northwest, and was probably causing widespread mortality in pole-sized stands as well as preventing natural regeneration from becoming established in many areas where it would have been expected historically (Mielke 1943, Moss and Wellner 1953). Large areas of M333d burned in the late 1800s and in 1910, so there were large expanses where white pine would have seeded in and been in sapling or pole-sized stands by the mid 1930s (Byler et al. 1994, Wellner 1970). Blister rust would have rapidly intensified in these stands, causing widespread mortality of these young trees.

As blister rust spread through the white pine region, even the largest trees were infected, and some had so many branch cankers that they died or were weakened so severely that they were predisposed to mortality by other agents (Buchanan 1938). Mortality is generally much slower in larger trees than on small trees due to the diameter that must be girdled before the tree is killed. However, even trees greater than 20 inches in diameter (measured at breast height–DBH) could be girdled in 20-30 years if heavily infected (Moss and Wellner 1953, Buchanan 1938).

Blister rust in whitebark pine (*Pinus albicaulis*)

White pine blister rust was first discovered on whitebark pine in 1926 in British Columbia (Lachmund 1928) and in Washington by 1931 (Childs et al. 1938). By the mid-1930s, "considerable infection" had been observed in the whitebark pine in the eastern portion of the St. Joe National Forest.

Even though whitebark pine is considered to be more susceptible to infection than western white pine (Hoff et al. 1980), overall mortality rates are generally believed to be lower in whitebark pine than in western white pine forests (Hoff and Hagle 1990). There are still stands containing large whitebark pine with little or no rust infection. Widespread effects of blister rust on whitebark pine forests have not been well quantified. Observations suggest that ribes plants are less abundant in these higher-elevation forests, so natural inoculum levels would be quite low. In addition, weather patterns and moisture levels may not be as favorable for infection as in lower elevation white pine stands. However, significant infection can occur from an occasional "wave-year," so it is not unusual to see entire stands of top-killed older trees and infection levels of 50-100 percent in small regeneration. It is possible that white pine blister rust may be severe enough to eliminate many pure whitebark pine stands and greatly reduce the whitebark pine component in high elevation mixed stands (Krebill and Hoff 1995).

Blister Rust Functions in Western White Pine

Historically, white pine forests developed after large fires created openings that were regenerated by seed from mature trees in the riparian areas that escaped the fires (Zack 1996). Mixed-species stands predominated early, but as white pine out-competed other species, many acres became predominantly white pine after about 150 years. White pine forests that escaped stand-replacing fires could last over 300 years, but were usually eventually killed by mountain pine beetles (Arno and Davis 1980, Wellner 1962, Fowells 1965, Zack 1996).

Since small trees are killed quickly by white pine blister rust, much of the natural regeneration which had historically resulted in white pine dominated stands has been lost at an early age (Byler et al. 1994). As a result, the successional pathways on many of the sites in this study have changed dramatically over a relatively short period of time. Before the introduction of blister rust, newly regenerated stands (structure class 1) with a white pine forest type (FT) would have grown into larger white pine stands (structure class 2 or 3) over 30-40 years. However, with most of the young white pine killed by blister rust, other species present grew up instead, resulting in a change in forest type. In stands that had a large component of other seral species (such as lodgepole pine or western larch), these other seral species benefited from the loss of white pine, which extended the early seral successional stage (Figure 6.8). However, in stands that contained large amounts of mid- to late-seral species such as grand fir, cedar, or hemlock, the loss of white pine tended to accelerate forest succession towards these more climax species.

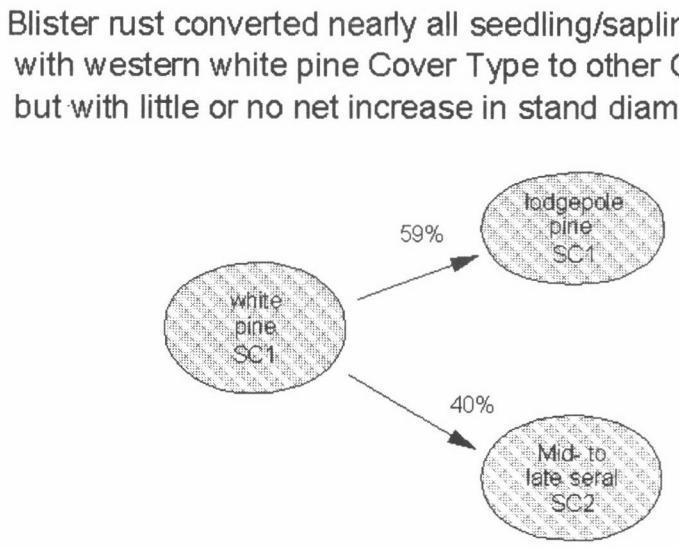
Blister rust converted nearly all seedling/sapling stands (SC1)
with western white pine Cover Type to other Cover Types
but with little or no net increase in stand diameters.
59%
lodgepole pine SC1
white pine SC1
40%
Mid- to late seral SC2

Figure 6.8: Conversion of white pine stands in structure class 1.

Pole-size stands (structure class 2) would be expected to have grown to dense mature stands (structure class 3) dominated by white pine over this 40-year period. But, with blister rust present, and depending on the original density of white pine and the intensity of the rust-caused mortality, most of these stands (78 percent of our sample) were prevented from following this historical pathway (Figure 6.9). "Pure" white pine stands (those with at least 66 percent white pine canopy cover), with high blister rust influence underwent radical changes in forest type and structure, while mixed stands with less white pine were affected to a lesser degree. Pure stands with low levels of blister rust influence suffer enough mortality to become mixed white pine forest types, while losses in mixed stands might not have much effect. Survival of other early seral species, such as lodgepole pine and western larch, tended to be enhanced by the loss of white pine.

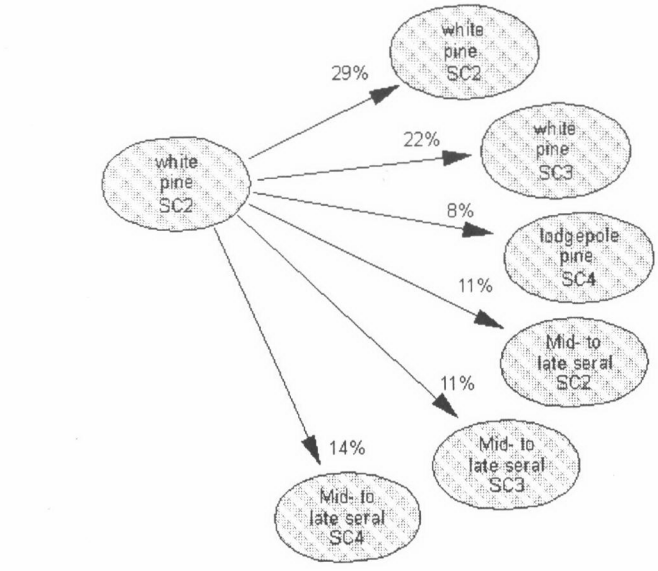

Figure 6.9: Conversion of white pine stands in structure class 2.

Larger white pine also are infected and killed by blister rust, but mortality rates are slower and confounded by mountain pine beetle and selective timber harvesting activities aimed at capturing white pine volume before it is killed by blister rust. Many large white pine were killed by blister rust during the 40-year analysis period corresponding to the blister rust spread though the West. These blister rust losses, coupled with accelerated harvesting, wildfires, and endemic losses from mountain pine beetle, largely eliminated the large-diameter stands of white pine by the 1970s.

In mature stands where white pine dominated, mortality from blister rust and other agents resulted in a change in forest type (Figures 6.10 and 6.11). In addition, it caused a structure change from class 3 to class 4 where the stand density is reduced and canopy becomes broken, or from class 3 to class 2 in stands where the largest trees are killed, leaving the understory. In stands with scattered white pine (where white pine were not abundant enough to be included in the forest type), losses might not result in a forest type change. However, even scattered white pine mortality contributed to a structure shift from class 3 to class 4 as irregular openings are created.

Most large-diameter, well-stocked western white pine stands (SC3) remained in this structure class although nearly 75% converted to mid or late seral species.

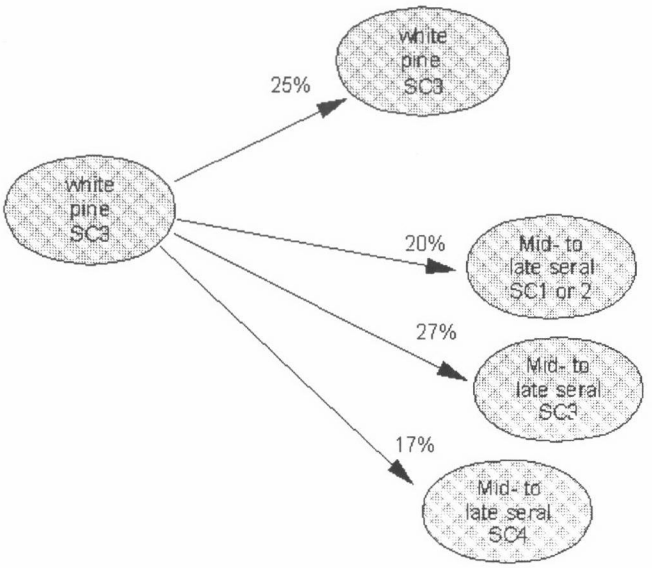

Figure 6.10: Conversion of white pine stands in structure class 3.

Large-diameter western white pine stands with low densities(SC4) tended to increase in density with about two thirds converting to mid or late seral species.

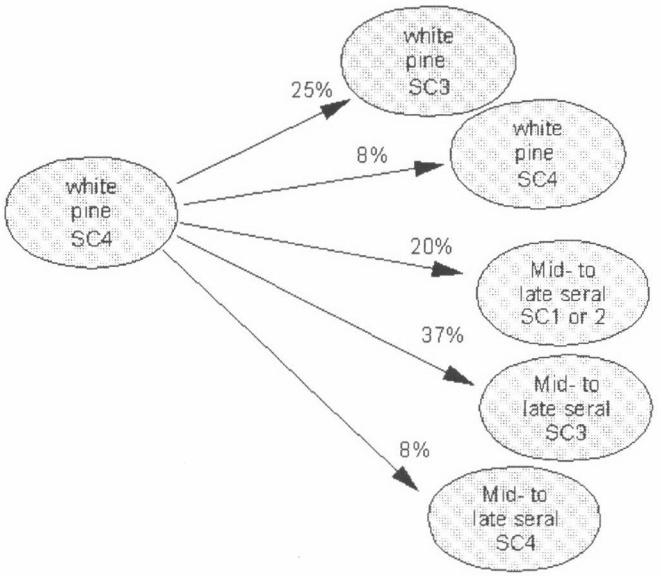

Figure 6.11: Conversion of white pine stands in structure class 4.

Since white pine is a long-lived seral species, the premature loss of white pine has had major consequences on historic successional pathways. The degree of change in successional pathways depended somewhat on the habitat type. In grand fir and subalpine fir habitat types, mortality from blister rust generally resulted in stands of more shade-tolerant species, which would tend to accelerate succession towards these climax species. In cedar and hemlock habitat types where Douglas-fir and grand fir are mid-seral species, the loss of white pine might tended to shift species composition to these mid-seral species. However, this result has lead to relatively unstable compositions because Douglas-fir and grand fir are very susceptible to root disease, and their increase has increased the extent and intensity of some of the more severe root disease functions.

Successional pathways which once included an extended white pine sere, sometimes producing old growth white pine stands, have been drastically altered resulting in abrupt transitions to mid- to late-seral tree compositions. As a result of these changes in successional pathways, forests which had historically contained a large portion of white pine have been replaced by forests dominated by grand fir, Douglas-fir, and western redcedar at lower elevations, and by western hemlock and subalpine fir at higher elevations.

Blister Rust Functions in Whitebark Pine Forests

In the few high elevation habitats where the climax species is whitebark pine, losses from blister rust would tend to reset succession to other seral species, especially lodgepole pine. However, whitebark pine is a seral in most of the few sites in this analysis which were suitable for whitebark pine, so blister rust tended to accelerate succession towards climax species, primarily subalpine fir (Figures 6.12 and 6.13). Whitebark pine is heavily dependent on fire for stand regeneration: after a burn, seeds are brought in by the Clark's nutcracker from trees that escaped the fire or adjacent unburned stands. This historical successional pathway was disrupted by blister rust in several ways. Blister rust may kill all or most of the nearby trees, virtually eliminating the seed source, or the upper (cone bearing) branches may be girdled by rust, which has essentially the same effect. When whitebark pine regeneration does become established, much of it is eliminated by blister rust. The result is both forest type and structure class changes.

Pathways from most sapling or pole stands (SC 1 or 2)
with a large component of whitebark pine lead to increases in subalpine fir
and increased relative importance of lodgepole pine. All remained in pole-size
structures.
"Fir" = subalpine fir

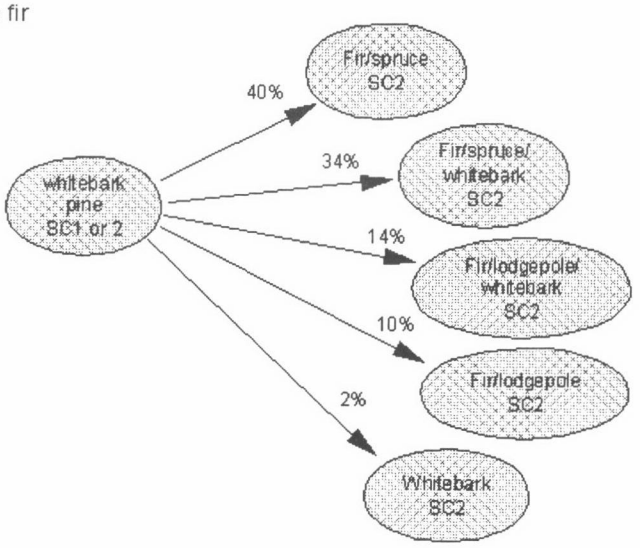

Figure 6.12: Conversion of whitebark pine stands in structure classes 1 and 2.

Large-diameter stands with a significant component of whitebark pine had fairly low densities (SC4). As the large whitebark pines died most stands became pole size class (SC2).
"Fir" = subalpine fir

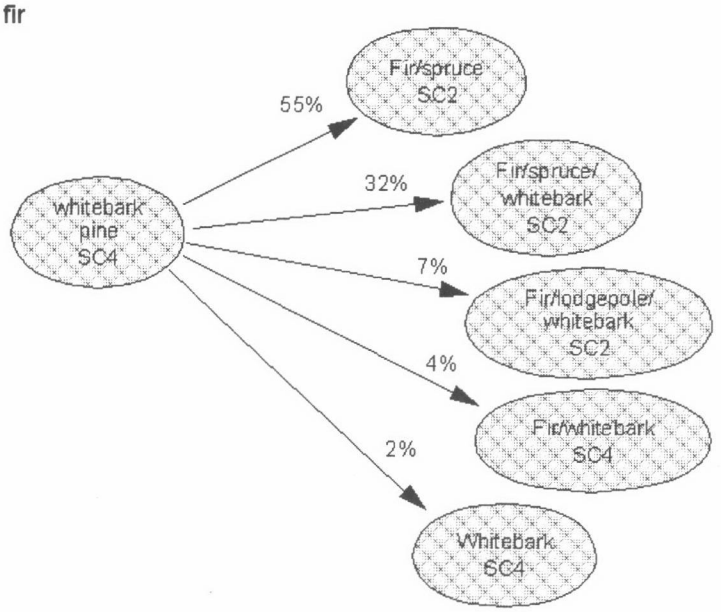

Figure 6.13: Conversion of whitebark pine stands in structure class 4.

Functions as Seen in M333d AND M332a

The results that follow are for analysis conducted on two of Bailey's ecosections, M333d and M332a. M333d covers much of the historical white pine range in northern Idaho and so will be discussed first. M332a includes the southern portion of the white pine range in Idaho, but with limited white pine forest types in M332a, our sample of these types is not nearly as robust in M332a as it is in M333d.

Ecosection M333d

WPBR hazard. In the 22,003 hectare sample of M333d that had been surveyed in both the 1935 era and the 1975 era, the highest WPBR hazard, level 4, was assigned to 46 percent of hectares. Hazard level 3 was assigned to 12 percent, level 2 to 27 percent and level 1 to only 1 percent. Fifteen percent of hectares were considered to have no blister rust hazard. Based on these high overall levels of hazard in M333d, it is not surprising that the accidental introduction white pine blister rust is considered the most important ecological disaster in the ecosection. The relationship between the rust hazard and the API for blister rust in stands with at least one live western white pine or whitebark pine, based on the current abundance and size of white pines in stands, follows the same trend in both the 1935-era and 1975-era survey data (Table 6.1). As the site hazard increased, the average API increased. However, as white pines disappear from stands it is possible that the highest hazard sites will eventually show the lowest average APIs and the lowest hazard sites, where white pines are expected to have higher survival rates, they will have higher APIs than the high-hazard sites.

Table 6.1: Average API for current white pine blister rust effect by site hazard rating for polygons with at least one western white pine or whitebark pine present.

WPBR Site Hazard	Proportion of Area	1935-era WPBR API*	1975-era WPBR API
2	.27	3.1	2.0
3	.12	5.1	5.1
4	.46	6.6	6.0

*The 1935-era WPBR API is the area-weighted average action probability index based on the 1935-era polygon class. The average index was calculated for polygon classes from the indices assigned to polygons using the 1975-era stand examination data for the sample of M333d.

Even when considering all polygons, even those with no western white pine or whitebark pine present in the 1975 era sample, the weighted average API was substantially higher for hazard level 4 sites (4.8) than for level 1 (0.0), 2 (1.3), or 3 (1.2) sites.

Cover types. The sample of ecosection M333d was 20,807 hectares with no evidence of tree harvests. Although western white pine cover type (code 1) was assigned to only 17 percent of hectares in the 1975 era, blister rust API, based on the presence of vulnerable white pine was greater than 0 on 39 percent of hectares. On the basis of polygon classes found in the 1935-era survey sample, 34 percent of hectares were white pine cover type and 47 percent of hectares had APIs which were greater than 0. The most common result of blister rust in stands from the 1935 era to the 1975 era (Table 6.2) was to move the species composition toward late-seral or climax components (57 percent of hectares). This was usually combined with the structure either remaining in seedling and sapling or pole structures for the 40 years, or losing the large-tree

components if they were mature, and moving backward to seedling/sapling or pole structures (40 percent of hectares that increased climax components). An ecologically important outcome was the conversion to other early seral cover types, particularly western larch and lodgepole pine. They were probably present among the species in the mixture that were classified as western white pine cover type in the 1935 era. This type of conversion was seen on 10 percent of hectares in the sample.

Table 6.2: Important cover type conversions in polygons with blister rust API greater than 0.

1935-era Cover Type	1975-era Cover Type	Proportion of 1935-era CT	Cover Change
White pine GE** 15%	White pine GE[1]** 15%	.32	Maintain seral
White pine GE** 15%	"Alpine"	.22	Increase climax
White pine GE** 15%	Western hemlock and grand fir GE 50% (at least one live western hemlock)	.19	Increase climax
White pine GE** 15%	Western redcedar and grand fir GE 50% (at least one live cedar)	.12	Increase climax
White pine GE** 15%	Lodgepole pine GE 50%	.06	Maintain seral
White pine GE** 15%	Douglas-fir GE 60%	.04	Increase climax
White pine GE** 15%	Western larch and Douglas-fir GE 75% with larch GE 10%	.03	Maintain seral
White pine GE** 15%	Western redcedar GE 50%	.03	Increase climax
Non-forested	Western redcedar and grand fir GE 50% (at least one live cedar)	.28	Increase climax
Non-forested	Douglas-fir GE 60%	.22	Increase climax
Non-forested	White pine GE** 15%	.16	Maintain seral
Non-forested	"Alpine"	.08	Increase climax
Non-forested	Ponderosa pine GE 25%	.08	Maintain seral
Non-forested	Western hemlock and grand fir GE 50% (at least one live western hemlock)	.07	Increase climax
Non-forested	Western larch and Douglas-fir GE 75% with larch GE 10%	.04	Maintain seral
Non-forested	Western redcedar GE 50%	.04	Increase climax

**GE = greater than or equal to

Forest types. In the 1935 era, over 50 percent of our sample of M333d was either a white pine forest type or had enough white pine for succession to be altered by white pine blister rust. About a third of the total area (6,581 hectares), had forest types that included white pine and about half of these probably had at least 66 percent white pine canopy cover, which is classified as white pine forest type. An additional 3,381 hectares were influenced by blister rust even though the forest type did not include white pine. Most of this acreage was from non-stocked areas in habitat types where white pine would be expected to regenerate, and the rest were stands in which white pine was present and suffered from blister rust but stocking levels were not high enough to be included as a forest type component (Table 6.3).

Whitebark pine forest types accounted for less than 0.2 percent of the hectares included in our sample of the 1935 era survey polygons. This sample is inadequate for proper analysis of transitions in these types. Succession effects of white pine blister rust in the white pine forest types served as a model for probable effects in the whitebark pine types. Transitions followed a parallel pattern in whitebark based on the density of whitebark pine in stands. Those with seral species, especially lodgepole pine tended to benefit from the loss of whitebark pine resulting in a prolonged seral stage, while those with subalpine fir or hemlock moved towards a more rapid succession to climax species.

After 40 years, the amount of white pine forest types had dropped from 33.5 percent to 5.1 percent of the total 20,807 hectares sampled (Table 6.3). This represents an 88 percent drop in white pine forest type during this 40-year period. All of the 2,958 hectares that were initially 'pure' (greater than 66 percent) white pine forest type transitioned to other forest types over the 40 year study period. Only 548 hectares (18 percent) retained enough white pine to remain a mixed white pine forest type; primarily forest types mixed with grand fir or Douglas-fir. The mixed-white pine forest types had an even lower percentage (12 percent) retain enough white pine to remain white pine forest types. Nearly 70 percent of the 3623 hectares that were mixed white pine forest types in the mid-1930s, transitioned to different forest types over the 40 years. All of these transitions were towards more shade tolerant species; the vast majority were to grand fir or Douglas-fir mixed species stands. Even though an additional 350 hectares (1.8 percent) transitioned to white pine from non-forest and other mixed stands that had blister rust influence, these represent only small percentages of what would have been expected historically.

Table 6.3: Losses of white pine from blister rust-affected stands. Hectares of rust-affected forest types in the 1935 era compared to hectares retaining a significant component of western white pine in the 1975 era.

1935-era Forest Type			1975-era Forest Types with WP	
	Ha.	% of Total Sample	Ha.	% of Total Sample
Pure western white pine	2,958	15.1	548	2.8
White pine-mix	3,623	18.5	455	2.3
Non-stocked with rust influence	2,043	10.4	144	.7
Other with rust influence	1,340	6.8	64	.3
Totals	9964	50.9	1211	6.1

Overall, grand fir, western hemlock and Douglas-fir appeared to have increased the most on sites formerly supporting white pine stands. Of the 6,011 hectares in our sample of M333d that were assigned white pine cover type in the 1935-era survey, 55 percent had grand fir as a forest type component in the 1975-era survey (Figure 6.14).

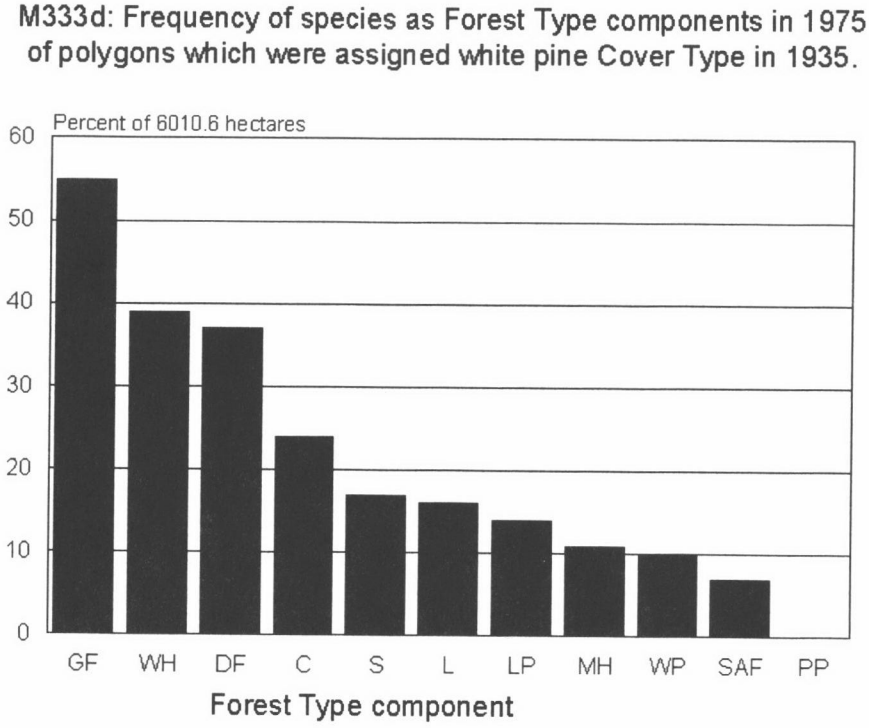

Figure 6.14: Ending frequency of species in white pine cover type.

Structure classes. Over 40 percent (2,772 hectares) of the white pine forest types were structure class 1 in the 1935 era, and 75 percent (1,991 hectares) transitioned to structure class 2 over the next 40 years (Table 6.4). Thirty-one percent of the 1935 era white pine forest types were structure class 4, and two thirds of these transitioned to structure class 3. Only 18 percent of the white pine forest types were structure class 3 in the 1935 era and most of this remained as structure class 3. After 40 years most hectares were in structure class 2 or structure class 3, which would have been expected without blister rust, but most of these had changed forest type. Over half of the white pine forest types had a high level of blister rust influence on successional pathways, indicating that blister rust induced both cover and structure changes that were different from those expected in the absence of blister rust. Another 35 percent had moderate rust influence, indicating that either the cover or the structure outcomes were altered. Only 11 percent were low, indicating a minor variation in the successional outcome with respect to tree species composition. This was usually manifest in a reduction in the proportion of white pine.

Table 6.4: Ecosection M333d: Transitions between the 1935 era and the 1975 era structural classes for hectares with white pine forest types.

1975-era Structural Class	1935-era Structural Class (hectares)				
	1	2	3	4	Totals (%)
0	35	0	11	4	50 (1%)
1	107	0	32	37	176 (3%)
2	1,991	215	224	249	2,679 (41%)
3	186	247	679	1,430	2,542 (38%)
4	354	165	247	368	1,134 (17%)
Totals %	2,673 41%	627 10%	1,193 18%	2,088 31%	6581 (100%)

When including the additional 3300 hectares where blister rust had an influence but were not white pine forest types, over half of the total (9946 hectares) were in structure class 0 or structure class 1 and nearly two-thirds of the hectares with high influence were in structure class 0 (27 percent) or structure class 1 (37 percent). (Table 6.5). Since infections on young trees are nearly always fatal, this is where we would expect the highest influence to occur. Structure class 3 with its larger trees was about evenly split between moderate and high rust influence, while structure class 4 was mostly moderate in rust influence.

Table 6.5: Relative probability of blister rust influence for hectares with blister rust influence for each structure class in 1935-era data for ecosection M333d.

1935-era Structure Class	Blister Rust Influence Probabilities (hectares)			
	High	Mod	Low	Total (%)
0	1,450	449	144	2,043 (21%)
1	2,024	454	472	2,950 (30%)
2	572	306	213	1,091 (11%)
3	580	519	100	1,199 (12%)
4	775	1,236	652	2,663 (27%)
Total %	5,401 54%	2,964 16%	1,581 30%	9,946

Habitat type groups. Since blister rust biology is influenced by habitat types, each habitat type (HT) group was looked at separately during this analysis. Nearly 70 percent of the 9,946 hectares influenced by white pine blister rust in the ecosection M333d sample were in the moderately cool/moist cedar-western hemlock habitat types (HT 5) (Table 6.6). About 25 percent were habitat type groups 7 or 9, the higher elevation cool, moist habitat types, while the remainder were primarily the moderately warm/moist grand fir habitat types.

The largest API values were obtained in cedar habitat types (HT 5) with a white pine forest type and in structure classes 1 and 2. This is where white pine historically achieved some of its greatest densities, so we would expect losses to have a major impact under these situations.

However, the proportion of hectares with potential rust influence was actually higher in habitat group 7 than 5 and even higher in habitat type group 9 (Table 6.6). This is primarily due to the large amount of non-stocked hectares in HTs 7 and 9 which were associated with rust influence.

Table 6.6: Hectares with different relative levels of blister rust influence in each habitat type group for ecoregion M333d.

1935-era HT Group	Total Hectares	Blister Rust Influence (hectares)			
		High	Mod.	Low	Total (%)
2-Douglas-fir Moderately warm/dry	1,981	69 (78%)	16	3	88 (1%)
3-Douglas-fir Moderately warm & dry	597	16 (44%)	0	20	36 (0%)
4-Grand fir Moderately warm/moist	2,094	248 (39%)	115	273	636 (8%)
5-Cedar/Hemlock Moderately cool/moist	8,695	3,395 (50%)	2,408	973	6,776 (68%)
7-Mountain hemlock cool/moist	3,081	795 (61%)	315	203	1,313 (13%)
9-Subalpine fir Cool/Moderately dry	2,722	878 (80%)	110	109	1,097 (10%)
Misc. groups not analyzed	399	--	--	--	--
Total	19,569	5,401	2,964	1,581	9,946

Most of the ecoregion falls in the cedar/hemlock habitat type group (HT 5), so the role of blister rust will be discussed in most detail with this group. Since the function of blister rust can vary with structure class, each structure class was examined in each habitat type group. Results will be discussed by each habitat type group and structure class, wherever important differences were found.

There were 6,776 hectares in HT 5 that had some blister rust influence (rated as high, medium, or low), and 30 percent of these were in structure class 1 (Table 6.7). This includes over 1,100 hectares of non-stocked land (structure class 0). Sixty-four percent of the non-stocked

hectares and 70 percent of the structural class 1 hectares had high blister rust influence, which is a reflection of the high mortality that can occur in young white pine. In spite of the blister rust influence, 77 percent (1,575 of 2,054) of these structure class 1 hectares managed to transition to structure class 2 during 40 years (Table 6.8). Historically most of these would have become forests dominated by white pine, but only 30 percent ended with white pine as even part of a mixed forest type.

Table 6.7: Ecoregion M333d, habitat type group 5: hectares with blister rust influence by structural class.

1935-era Structure Class	Blister Rust Influence (hectares)			
	High	Mod	Low	Total (%)
0	717	318	92	1,127 (17%)
1	1,428	355	271	2,054 (30%)
2	361	265	83	709 (10%)
3	310	470	63	843 (12%)
4	579	1,000	464	2,043 (30%)
Total %	3,395 50%	2,408 36%	973 14%	6,776 100%

Over 80 percent of the 6,776 hectares with rust influence transitioned towards a climax cover type, while most of the rest maintained a seral cover. In terms of structure trends, 31 percent "stalled", 16 percent prevented canopy closure 8 percent maintained the same structure class as expected 20 percent increased density, and only 17 percent followed a normal progression.

Table 6.8: Ecosection M333d, habitat type group 5: transitions in structure class of hectares with blister rust influence between 1935-era and 1975-era surveys.

1975-era Structure Class	1935-era Structure Class (hectares)					
	0	1	2	3	4	Totals (%)
0	48	16	0	4	0	68 (1%)
1	378	91	0	0	46	515 (8%)
2	454	1,575	211	86	185	2,511 (37%)
3		137	341	538	1,388	2,404 (35%)
4	247	235	157	215	424	1,278 (19%)
Total %	1,127 17%	2,054 30%	709 10%	843 12%	2,043 30%	6,776 (100%)

Cover types. The WPBR hazard for this habitat type group is 4. The average API for the 22,003 hectare sample that was surveyed in both the 1935 era and the 1975 era was 3.3 in the 1975 era and the calculated average based on polygon classes was 4.8 for these polygons in the 1935 era. The decline in API was due to the decrease in the amount of cover types in which western white pine and whitebark pine were important species (Table 6.9). The assignment of APIs that are greater than 0 indicates that there were live western white pine or whitebark pine in the stands. Where the white pine cover type was not assigned, the white pines made up less than 15 percent of the stand (see the Methods chapter, cover type classification, for more detail).

Table 6.9: Cover types in habitat type group 5 with at least one live western white pine or white bark pine present. Proportion in the 1935 era and the 1975 era for the same 22,003-hectare sample.

Cover Type	1935-era Survey	1975-era Survey
White pine GE 15%	.80	.54
Non-forested	.16	.01
Western redcedar and grand fir GE 50% (at least one live C)	.00	.19
Western hemlock and grand fir GE 50% (at least one live WH)	.02	.13
Subalpine fir and other "alpine" species	.00	.12

About a third (33 percent) of the hectares that were classified as white pine cover type in the 1935 era were still classified as white pine in the 1975 era. Grand fir mixed with western hemlock (22 percent), grand fir mixed with western redcedar (17 percent), and subalpine fir mixtures (14 percent) were the cover types assigned to most of the rest of the hectares in the 1975-era survey that had started as white pine cover types. When the 1975 era white pine cover types are projected forward, the pattern of cover type changes remains much the same (Table 6.10).

Table 6.10: The fate of white pine cover types in habitat type group 5. Ending cover types 40 years after classification as white pine cover type. Proportion of the hectares starting in white pine cover type in the 1935 era.

Ending Cover Type	1935 to 1975 (actual)	1975 to 2015 (projected)
White pine GE 15%	.36	.41
Western hemlock and grand fir GE 50% (at least one live WH)	.24	.18
Western redcedar and grand fir GE 50% (at least one live C)	.15	.24
Subalpine fir and other "alpine" species	.15	.09
Western redcedar GE 50%	.04	.05
Douglas-fir GE 60%	.02	.01
Western larch and Douglas-fir GE 75% with larch GE 10%	.01	.00

Non-forested polygons (those with fewer than 20 live trees per acre and less than 2000 bd.ft./acre) were the only other important cover type (16 percent) in the sample of polygons in HT group 5 that had at least one live white pine in the 1935 era. Cover types on these hectares in the 1975 era were mostly grand fir mixed with western redcedar (28 percent), Douglas-fir (22 percent), or western white pine (16 percent).

Forest types. Historically the Douglas-fir/white pine mixed stands would have converted to a more pure white pine stand due to Douglas-fir mortality by root disease. Now that white pine has also been removed because of blister rust, many of these stands have transitioned primarily to cedar, hemlock, and grand fir forest types. However, if other seral species such as western larch were present, they may have been taken over some of these sites. The combined effect of these agents removed white pine, Douglas-fir, and grand fir from these stands, creating more opportunities for larch.

In structure class 2, there were a total of 1,428 hectares in this habitat type group (5). Almost half (709) were influenced by blister rust, mostly to a moderate or high level (Table 6.11).

Nearly 30 percent of the 1,428 hectares were white pine (259 hectares) or mixed white pine (159 hectares) forest types in 1935-era data. Within 40 years, all the pure white pine forest type were gone, and only 10 percent (79 hectares) were mixed white pine forest types that all had low blister rust influence. Seventy-seven percent of the hectares with some blister rust influence transitioned to cedar/hemlock/grand fir forest types, and the remaining 13 percent transitioned to Douglas-fir/grand fir forest types.

The other half of the hectares in this structure class and habitat type group that had no blister rust influence nearly all ended up as cedar/hemlock or mixed stands of larch, lodgepole, and grand fir. All the hectares that were cedar or hemlock in the 1935 era transitioned to

cedar/hemlock forest type, and over half (60 percent) of those that had larch components had the larch replaced by cedar or hemlock.

In structure class 3 and structure class 4 there were 2,886 hectares with blister rust influence and 58 percent (1,675) of these hectares were also influenced by mountain pine beetle. If these areas were grand fir/white pine forest type, none of it ended as white pine or Douglas-fir forest type because of root disease and blister rust. However, 97 percent remained structure class 3 or structure class 4, so these agents tended to push these areas towards climax species. However, if the area was originally a white pine or mixed white pine forest type (628 hectares), much of it transitioned to a Douglas-fir forest type. These were also areas that had very low root disease ratings.

Only three percent of the 2,889 white pine forest type hectares that were in structure classes 2-4 remained white pine forest types. This is a major departure from what would have been expected historically: white pine should have become more and more dominant with age instead of less and less. This is illustrated by the results of the few hectares of white pine forest type that had low blister rust influence. Although no pure white pine stands remained even with low blister rust influence, over 75 percent stayed mixed white pine forest type, and 87 percent of all white pine or white pine-mix forest type that had low blister rust influence remained white pine-mix forest type. The stands with low blister rust influence also had a higher proportion follow expected transitions in structural classes.

Cool and moist habitat types (HT 7)

Forty-three percent of the total area of habitat type group 7 (1,455 of 3,383 hectares) was influenced by blister rust to some level (Table 6.11). The site hazard for this habitat type group is 2. The calculated weighted average API for blister rust in the 1935 era was 1.4 overall and 5.0 for polygons which had white pine cover type. In the 1975 era, the overall average API as 0.3 and the average for polygons with white pine cover type was 4.3. The primary reason for the difference between the API in the 1935 era and that in the 1975 era in white pine cover type was that the 1975 era stands were more mature, reducing the probable effect of blister rust. At the same time, the proportion of white pine cover type was drastically reduced, further reducing the overall influence of blister rust. According to the 1935 era polygon classes, about 26 percent of hectares should have had fairly heavy blister rust infection with significant components of white pines in the stands. By the 1975 era, the proportion of stands with potential for heavy blister rust and significant components of white pines had dropped to a little over 5 percent. All of the polygons which were in classes which average more than 0 for API in the 1935 era had white pine cover type. Most of the white pine cover type converted to subalpine fir mixtures or lodgepole pine, but 13 percent remained white pine cover type (about 5 percent of this habitat type group overall).

From 28 percent white pine cover type in the 1935 era, the proportion of white pine cover type shrunk to only 6 percent in the 1975 era. If this trend continues, there is projected to be only 4 percent white pine cover type in this habitat type by 2015. Most of the hectares (59 percent that were white pine cover type in the 1935 era had converted to subalpine fir mixtures by the 1975 era. Lodgepole pine cover type also gained some area, 228 hectares (24 percent of the original white pine type), by the 1975 era from what had been white pine cover type. Only 13 percent of what had been white pine cover type, remained so.

The calculated proportion of white pine forest type this represented in the 1935 era (based on polygon class) was 27 percent, and over the next 40 years, this was reduced to just 2 percent.

Either way it is viewed, the white pine component of this habitat type has been reduced drastically. The few hectares that remained white pine forest type were primarily in the smaller structure stages that transitioned from structure class 1 to structure class 2 or from structure class 2 to structure class 3. This probably represents a few hectares that were in low hazard sites where enough white pine survived 40 years to remain a white pine forest type.

Table 6.11: Ecosection M333d: cool and moist habitat types (HT 7); hectares with blister rust influence by 1935-era structure class.

1935-era Structure Class	Blister Rust Influence (hectares)			
	High	Mod	Low	Total (%)
0	272	103	24	399 (30%)
1	211	38	97	346 (26%)
2	84	0	75	159 (12%)
3	98	20	0	118 (9%)
4	130	154	7	291 (22%)
Totals %	795 61%	315 24%	203 15%	1,313 100%

Stands that were in a non-forested condition at the 1935-era survey were also significantly influenced by white pine blister rust. Based on the relative frequency of white pine and white pine-mixed forest types in structure classes 1 and 2 in the 1935-era sample, roughly half (45 percent) of the non-forested hectares would have been expected to become stocked with white pine and mixed types containing significant components of white pine. Only 3 percent of hectares that were non-forested in the 1935 era contained significant white pine at the 1975 era resurvey and it was all from areas that had low blister rust influence. A relatively high proportion (40 percent) of the stands that were non-forested in the 1935 era had converted to climax species composition in structure classes 1 or 3 by the 1975 era. These stands had become subalpine fir, mountain hemlock or grand fir.

On the portion that was structure class 1, blister rust was the only significant influence on 84 percent of the hectares; root disease was significant on the remaining 16 percent. By contrast, root disease was significant on 43 percent of hectares where blister rust had no influence. This is probably because the areas with little rust influence had more of the root disease susceptible species. During the 40 year period over 80 percent of this class underwent normal transitions in structure class, although none of it remained a white pine forest type. Cover changes were mostly towards climax species.

There were not many hectares in the other structure classes, but they all tended to transition towards climax species. Some structure class 2 areas with lodgepole pine and white pine had mountain pine beetle in the lodgepole pine broke up into structure class 4 or reverted to structure class 1 with both white pine and lodgepole pine dropping out of the forest type. None followed normal succession to structure class 3.

However, lodgepole pine was particularly likely to be favored in stands starting in the seedling/sapling or pole-size structure classes. There were 249 and 84 hectares, respectively, in

structure classes 1 and 2 of habitat type group 7, with high or moderate blister rust influence (Table 6.11). Of these, 28 percent of structure class 1 and 71 percent of structure class 2 maintained or increased seral species other than western white pine, especially lodgepole pine.

Structure classes 1 and 2 were typically seral species; 63 percent were seral without significant climax species composition. In contrast, only 8 percent of structure classes 3 and 4 were seral species without significant climax components. White pine blister rust and root diseases are the main factors that are influential in the small structure classes. They are particularly likely to have controlled the shift away from seral white pine and Douglas-fir components in stands that had been non-forested in the 1935 era.

Although the sample size for structure class 3 and structure class 4 is relative small, nearly all stands with structure class 3 that had a significant white pine component had high or moderate blister rust influence, and all of the structure class 4 that had high or moderate blister rust influence were in a white pine forest type. Both structure class 3 and structure class 4 moved strongly toward more climax species composition as blister rust killed the white pine components. In these stands, subalpine fir and mountain hemlock were most likely to increase. It is likely that there was little by way of other seral species to be maintained in these more mature stands in the 1935 era.

Where blister rust had a moderate or high influence in this habitat group, it tended to be the dominant, and often only, agent driving changes in both cover and structure.

Cool and moderately dry habitat types (HT 9)

According to 1935-era polygon classes, 49 percent of hectares probably had minimum probable effect from white pine blister rust. Moderate levels of effect may have been seen on 46 percent (APIs 1 and 2), and very high APIs (levels 6,7 and 8) were expected on 5 percent of hectares. As the white pine components have declined in the sample, the API have also declined. In the 1975 era sample, 63 percent of hectares had an API of 0: no probable effect. An additional 30 percent had an API of only 1, the remaining 7 percent had high APIs of 6, 7 or 8. Of the 51 percent of hectares that had some level of expected blister rust activity, 31 percent were subalpine fir mixed cover types, 26 percent were lodgepole pine cover type, 25 percent were white pine cover type, and 10 percent was larch/Douglas-fir cover type. White pine cover type mostly converted to subalpine fir or lodgepole pine cover types with only about 15 percent of this type remaining white pine cover type in the 1975 era.

Blister rust influence was strongest in structure classes 0, 1, and 3, and relatively low in classes 2 and 4 (Table 6.12).

Table 6.12: Ecosection M333d, subalpine fir/mountain hemlock habitat type group (HT 9): Hectares with blister rust influence by 1935-era structure class.

1935-era Structure Class	Blister Rust Influence (hectares)			
	High	Mod	Low	Total (%)
0	451	28	28	507 (46%)
1	198	61	11	270 (25%)
2	32	14	42	88 (8%)
3	172	0	14	186 (17%)
4	25	7	14	46 (4%)
Total %	878 80%	110 10%	109 10%	1097 100%

Root disease was also a strong influence in this habitat type group, so to understand the function of blister rust it is necessary to tease the pathways apart. Blister rust had about the same probability of occurring in a polygon whether root disease was a significant influence or not. But the outcomes in polygons with high to moderate influence of both agents were somewhat different from those where only blister rust was a significant influence. In areas where neither agent was significant, the trend was overwhelmingly (71 percent) toward larger size classes and denser stands. About half of these areas trended towards climax species while the other half maintained their Douglas-fir or lodgepole pine seral components throughout the 40-year period.

Stands which had moderate or high influence from both blister rust and root disease made up only 7 percent of the 1935-era sample. The great majority of these stands (80 percent) transitioned to an earlier structure class than they were in the 1935 era. Most of these had started in structure class 3 (64 percent). Cover changes were primarily towards more climax species (66 percent). One-fourth increased in non-white pine seral species, primarily lodgepole pine and western larch.

Stands with high or moderate blister rust influence but with low or no root disease influence made up 29 percent of the hectares in this habitat type group. Nearly all (90 percent) of these stands transitioned towards increased size and stand density. The species composition of about half moved towards climax, species while the other half tended to maintain Douglas-fir and lodgepole pine seral components regardless of the 1935-era structure class.

It appears that the overall influence of blister rust in habitat type group 9 is to remove the white pine component from stands without otherwise altering the general successional trends. However, when blister rust is combined with significant root disease influence, they tend to reset the structure class to seedling/sapling or pole classes while pushing the composition towards late seral species (about 66 percent of hectares) or increasing the Douglas-fir and western larch early seral component (about 33 percent of cases).

Moderately warm and moist habitat types (HT 4)

There were a total of 2,405 hectares in this habitat type group, and 30 percent had some level of blister rust influence (Table 6.6). The 1935-era survey had 350 hectares of white pine or

white pine-mixed forest type but by the 1975 era white pine had been eliminated as a component of any forest type. The most frequent API in this habitat type group in the 1975 era was 0 (89 percent), and the remaining 1 percent of the hectares had an API of 5. Of the 602 hectares that were in cover types which had an average API of 5 in the 1935 era, 69 percent were white pine cover type and 31 percent were larch/Douglas-fir cover type. Stands in both of these cover types with structure class 1 tended to end with more western larch if they had a significant blister rust influence. The loss of white pine from structure class 2 tended to result in an increase in lodgepole pine unless they had a grand fir component, in which case the grand fir tended to increase. Thirty-eight percent of the hectares with white pine cover type in the 1935 era were still white pine cover type in the 1975 era. The remainder had converted mostly to larch/Douglas-fir (15 percent), lodgepole pine (13 percent), Douglas-fir (13 percent), or grand fir (11 percent) cover types.

Structure class 3 stands with blister rust influence that had a grand fir (climax) component in the 1935 era overwhelmingly transitioned to earlier structure class and maintained or increased the seral composition. Douglas-fir and larch were the main serals that gained. However, all of the polygons with blister rust influence also had moderate mountain pine beetle ratings and moderate to high root disease severity ratings which would also have contributed to these transitions. The combination of blister rust and mountain pine beetle probably eliminated most of the large white pine in structure class 3, and set stands back to earlier structure classes while favoring the seral species.

Hectares in structure class 4 with blister rust influence all changed to grand fir or Douglas-fir forest types. The primary function of blister rust was to increase the climax species composition of the stands (62 percent of hectares). The most important structure effect was to prevent canopy closure (72 percent of hectares). Most of the area in this structure class began as a white pine mix forest type (with Douglas-fir or grand fir). Root disease was high or moderate in most of these stands after the loss of white pine, so stand closure was probably prevented by root disease mortality in the Douglas-fir and grand fir. The outcome is root disease patches with low density and smaller diameter, probably younger Douglas-fir and grand fir.

Results from Ecosection M332a

There were almost no API values for blister rust generated in ecosection M332a. However, the API values are based on current stand conditions, and most of the white pine has either been logged, burned or killed by blister rust, so very few stands had enough white pine remaining to meet the criteria for even minimal API values. The fact that there were no white pine forest types in the current data is a major change from what might have been expected.

In our sample of M332a, there were 4,328 total hectares. Thirteen percent (557 hectares) had a 1935-era forest type that included white pine (10.2 percent) or whitebark pine (2.7 percent), and nearly all of this had some level of blister rust influence (Table 6.13). After 40 years, none of the original white pine forest types were considered white pine or whitebark pine forest types, and nearly half of the whitebark-mixed forest types lost their whitebark pine component. Although a small amount of stands transitioned into whitebark pine that were originally subalpine fir/lodgepole pine forest type or non-forested land, no acreage transitioned into white pine.

In the lower elevations, where the original forest type was white pine/Douglas-fir, 90 percent of the area transitioned to a cedar or cedar/Douglas-fir mix, while the rest transitioned to a Douglas-fir or Douglas-fir/grand fir mix forest type. In the higher elevations, stands that were originally white pine/Douglas-fir/lodgepole pine transitioned to stands with a forest type of

alpine fir or mountain hemlock. The whitebark pine mixed forest types also transitioned to climax species of alpine fir or mountain hemlock.

Nearly half of the white pine/whitebark pine forest types area was found in habitat type groups 4 and 5, while the rest was fairly evenly distributed in habitat types 7, 9, and 10 (Table 6.13).

Table 6.13: Ecosection M332a, 1935-era habitat type group (HT) and structure classes for hectares with white pine or whitebark pine forest types.

1935-era HT	Total Hectares	1935-era Structural Class (hectares)				
		SC 1	SC 2	SC 3	SC 4	TOTALS (%)
4	347	5	39	38	46	128 (23%)
5	1,199	6	140	0	0	146 (26%)
6	8	0	0	0	2	2 (0%)
7	685	0	28	0	75	103 (19%)
9	771	0	0	4	86	90 (16%)
10	171	88	0	0	0	88 (16%)
TOTALS	*4,328	99 (18%)	207 (37%)	42 (8%)	209 (37%)	557 100%

*excludes 1,147 hectares in these habitat type groups with no blister rust influence.

Over 90 percent of cedar/hemlock habitat type group (HT 5) and 61 percent of grand fir habitat type group (HT 4) had moderate or high blister rust influence while blister rust influence on the other habitat types was generally low.

Since there were no true whitebark pine habitats sampled, the loss of white pine or whitebark pine resulted in a change of forest type to more shade-tolerant species in every habitat type group. The lower elevation habitat type groups transitioned to cedar/hemlock/Douglas-fir forest types while the higher elevation habitat type groups became predominantly subalpine fir or mountain hemlock. This resulted in a push to climax in about 75 percent of the hectares and stalling of succession in the 25 percent of hectares in the cedar and hemlock habitat type groups (HT 5 and 6).

Even though white pine was lost from young stands, 95 percent of the hectares that were structure class 1 in the 1935 era transitioned to structure class 2 during this 40-year analysis period (Table 6.13). However, they all changed forest type from white pine, so there must have been enough other species present to compensate for the loss of white pine. Fifty percent of the structure class 2 hectares transitioned to structure class 3, which is less than would have been expected. Another 25 percent of the structure class 2 transitioned to structure class 4, while most of the remainder were either logged (became non-forest) or stayed in structure class 2.

Nearly all of the hectares that were structure class 4 in the 1935 era had low blister rust influence, while most of the structure class 1 and structure class 2 hectares had moderate or high

blister rust influence. Therefore, changes in structure class or forest type for structure class 4 hectares are more likely due to insects or other agents than blister rust.

Only a small area, (3 percent of hectares), had both blister rust and mountain pine beetle ratings, so it is difficult to establish any meaningful relationships between these two agents. Since mountain pine beetle tends to attack larger trees, it is not surprising that there were no hectares of structure class 1 or structure class 2 with mountain pine beetle ratings, and all the high bark beetle ratings were in structure class 3 where white pine would be expected to be the most susceptible to bark beetles.

Discussion

Our data analysis has shown that over a 40-year period, there has been a severe impact on white pine and whitebark pine due to white pine blister rust. It has successfully short-circuited many historical successional pathways, causing changes far greater than ever recorded historically. Since this is an introduced disease, there was very little native resistance, so it has had a much greater effect on ecosystems than periodic outbreaks of native agents such as mountain pine beetle.

White pine forest types were historically common, especially in M333d, but by the 1975-era survey, there were no areas where white pine was the dominant species and very few where white pine was one of the top two or three species. Even based on cover type classification, which requires only 15 percent western white pine, the abundance of white pine cover type was halved in just 40 years (Figure 6.7). Most of the white pine cover types were converted to forest types that included grand fir, western hemlock, Douglas-fir, and/or western redcedar (Figure 6.14). This was especially true of polygons which were in the smaller structure classes in the 1935 era. (See Table 2.6 for explanation of forest type classification.)

The dramatic loss of white pine has continued since the 1975 era. Brown and Chojnacky (1996) reported that white pine forest type had dropped 93 percent in Idaho between 1954 and 1991, while spruce-fir (subalpine fir, grand fir, Engelmann spruce) increased 177 percent. They also reported that white pine was the only species that showed a net loss in growth during this 37-year period, primarily due to blister rust.

Although transitions in structure classes from structure class 1 to structure class 2 and structure class 2 to structure class 3 appear to be normal for much of the analysis area, the forest types usually changed. This means that there must have been enough other species (usually shade-tolerant climax species) present to compensate for the loss of the white pine component. Historically, we would have expected many of structure class 3 or structure class 4 forests to be dominated by large mature white pine and remain unchanged for long periods of time. Large stands would usually burn or be subject to large bark beetle outbreaks, but some would reach advanced ages (300 or more years).

We did find an overall increase in structure class 3 in M333d from the initial conditions (38 percent from 18 percent) but not as forest types that included white pine. This increase is most likely due to increasing density of shade-tolerant species as white pine was eliminated. The transition from structure class 4 to structure class 3 in M333d is probably also a result of shade-tolerant species filling in as white pine was removed by blister rust or mountain pine beetle.

Blister rust also had considerable influence on stands that were not white pine forest types but contained at least some white pine. At least some of these stands would have traditionally transitioned to white pine forest types as other agents removed other competing tree species. However, blister rust prevented many of these stands from becoming white pine forest types, and

may also have influenced their structure, particularly when a stand progressed from structure class 1 or structure class 2 to structure class 4 rather than the expected structure class 3.

Most of high blister rust influence was associated with the small structure classes (structure class 1 and structure class 0) which is where we would expect blister rust to have the biggest impact. If small white pine are eliminated at this stage, many of these areas will not have a chance to mature into stands with a high proportion of white pine.

Current Trends

As white pine has been lost from many areas, it has been replaced by shorter-lived species such as Douglas-fir and grand fir. These species are highly susceptible to other insect and disease agents, and we have already noticed increased activity of other agents such as bark beetles and root diseases in these species. Many areas with serious disease problems have developed in areas that were historically white pine stands. In the past, root disease would have had a desirable effect on stands by removing some of the competing vegetation from the white pine. Root disease is still removing grand fir and Douglas-fir, but now that white pine has largely been removed, mortality of Douglas-fir and grand fir is not considered desirable, and often results in undesirable openings in stands. However, in a small proportion of stands where other serals such as larch and lodgepole pine occur, they have benefited from the multiple losses from blister rust and root disease.

If we are to rehabilitate forests to be more reflective of historic forest types and structure classes, it will be important to re-establish white pine on many areas. An intense genetics breeding program has been established to take advantage of the small amount of natural resistance to blister rust (Bingham 1983). However, in recent years we have observed higher than normal expected levels of infection in some plantations of improved stock. While the exact reason for this is currently being researched, the fact that this is occurring serves to emphasize that the genetics breeding program will require a long-term effort to identify and incorporate desirable resistance traits.

Long-term effects on white bark and limber pine ecosystems are not entirely known, but many stands have very high levels of infection. Since these high elevation pines play important roles in wildlife ecosystems such as the Clark's nutcracker and grizzly bear, extensive losses to blister rust could have long term impacts that may not be understood or recognized at this time.

ROOT DISEASE FUNCTIONS AND SUCCESSION REGIMES

By Susan Hagle

The root pathogens are an influential group of organisms in Idaho north of the Salmon River and Montana west of the Continental Divide. They have the potential to be very old, in excess of 1,500 years, and to respond slowly to changes in food supplies. They will live long after their host has died by slowly decomposing the remains of the root systems (Tkacz and Hansen 1982, Greig and Pratt 1976, Hagle and Shaw 1992). They are capable of utilizing many species of live and dead tree tissues (and perhaps other plants). *Armillaria ostoyae*, *Phellinus sulphurascens* (formerly *Phellinus weirii*, Douglas-fir type), *Heterobasidion annosum*, and *Phaeolus schweinitzii* are the most common and pathogenic root disease-causing fungi in ecosections M332a and M333d. Other, less pervasive or less pathogenic root pathogens include *Inonotus tomentosus*, *Resinicium bicolor*, *Perenniporia subacida*, and *Ceratocystis* sp. Extensive excavation of root systems on a site often reveals several of these fungi.

The way in which these pathogens act independently is poorly understood because of their strong tendency to occur together on sites. But the way in which this "consortium" of fungi interact with their substrates and physical habitats is visible on the landscape. The tree species most readily killed, the relative extent of root infection of the various tree species, the actual and relative rates of tree mortality, the effects of tree density through time, the longevity of fungus mycelia in dead root tissue, the cumulative effects of tree death and regeneration, and the resultant long-term trends of both fungus and tree biomass are observable or interpretable for the consortia. For this reason, because the ecology and functions of these root pathogens are not separate in the real forest, the regimes which describe their successional dynamics are not presented here by pathogen species.

The time scales necessary to describe the successional regimes of root pathogen-influenced forests generally must span at least several generations of trees to fully account for the slow changes in the biomass of an individual fungus. The fungus biomass can greatly influence the successional pathways or rates. Habitat type is a site classification system that is based on succession. Habitat type groups used in this analysis are among the significant factors influencing root disease severity (Table 6.15 and 6.16).

The prevalence of root disease in both ecosections is evident in the high frequency of significant root disease effects in the 1975 era samples (Figure 6.15). Only 2 percent and 6 percent of non-harvested hectares of M332a and M333d sample polygons, respectively, were assigned severity level 0. The rating of '0' does not imply that the pathogens are not present, only that effects of root disease were not visible in the aerial photographs. The most severe level of root disease was also uncommon, occurring in only 1 percent of ecosection M332a (Table 6.14) and 3 percent of M333d. These rates agree closely with earlier studies by James et al. (1984), Williams and Leaphart (1978) and Byler et al. (1990). James et al. found 1.2 percent of the Nez Perce National Forest (mostly in ecosection M332a), 0.4 percent of the Clearwater National Forest (in ecosections M332a and M333d), 0.5 percent of the St. Joe National Forest, 5.1 percent of the Couer d'Alene National Forest, and 1 percent of the Lolo National Forest (in ecosection M333d) to be in root disease patches (roughly equivalent to classes 8 and 9). Williams and Leaphart (1978) reported finding root disease patches on 5.1 percent of the Couer d'Alene National Forest. Root disease severity levels 8 and 9 were assigned to 3 percent of hectares of our sample in M333d. Byler and others (1990) reported finding 1.2 percent of the Lolo National Forest in root disease patches. These percentages compare roughly to 1 percent of our M332a sample and 3

percent of M333d sample assigned severity classes 8 and 9. James and others also reported finding heavy scattered mortality from root disease on 33.3 percent of the Nez Perce National Forest and 13.3 percent of the Clearwater National Forest. Byler and others found significant root disease impact on 18.8 percent of the Lolo National Forest.

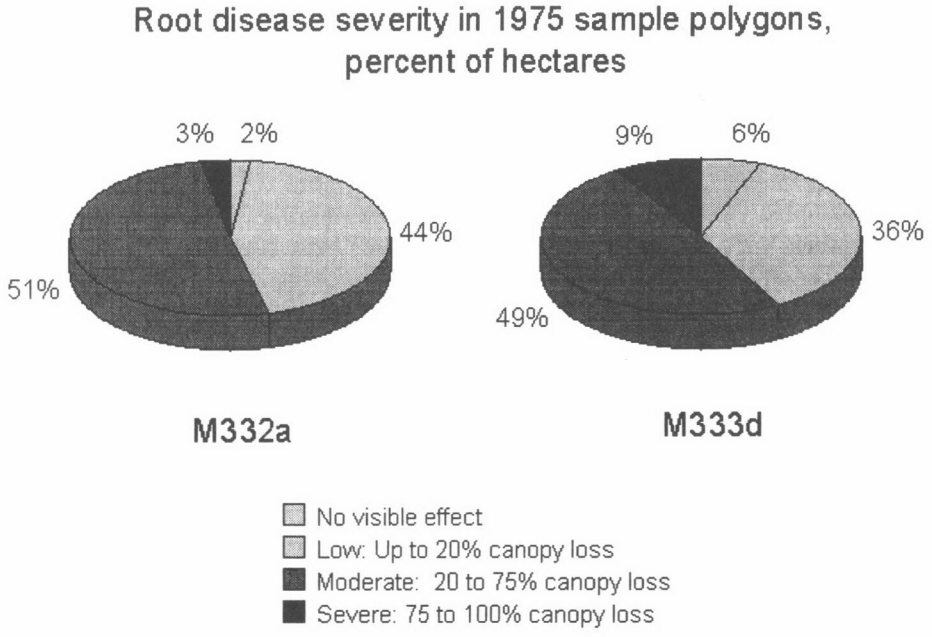

Figure 6.15: Root disease severity in 1975-era polygons.

Table 6.14: Frequency of root disease severity classes assigned to polygons in ecosections M332a and M333d based on 1975-era photographs.

Root Disease Severity Class	M332a Percent of 7,500.4 ha. Sample*	M333d Percent of 2,1166.5 ha. Sample*
0	2	6
1	7	1
2	20	17
3	15	18
4	18	21
5	20	15
6	15	13

7	2	7
8	1	2
9	0	1

*Excluding polygons with moderate to heavy harvest levels.

Of the 22,832 hectares in the 1975 era survey of M333d, the average root disease severity assigned was 4.0. Of the 8,134 hectare sample of M332a, the average root disease severity was 3.9. This represents a moderate level of severity overall in both ecosections. Severity classes 2 and 5 were the most commonly assigned classes in M332a, and classes 3 and 4 were common in M333d. Classes from 2 to 5 were common in both ecosections, a low to moderate range of disease severity. Disease severity levels 6 and above, indicating at least 50 percent reduction in forest canopy caused by root disease, were assigned to 18 percent and 23 percent of hectares, respectively, in ecosections M332a and M333d. Disease severities varied greatly with both ecosections, however, and several factors were found to significantly influence disease severity in polygons.

Polygon class attributes related to root disease severity

There were several significant factors related to disease severity (Tables 6.15 and 6.16). The habitat type group, forest type, and structure class were independently significant factors associated with root disease severity. The combination of habitat type group and structure class was also a significant factor in M332a, and forest type combined with structure class was significant for M333d. It is interesting to note that although the forest type was a highly significant factor for predicting root disease severity, the cover type was not significant in M332a and significant only at the 90 percent level in M333d. With only 11 cover types in M332a and 12 in M333d compared to 57 forest types for the same polygons in M332a and 118 forest types for the polygons in M332a, there was apparently too little resolution in the cover types to detect significant relationships with root disease severity.

Table 6.15: Results of analysis of variance using habitat type group, cover type and structure class to predict root disease severity levels.

	M332a		M333d	
Factors	**Degrees of Freedom**	**Probability > F**	**Degrees Freedom**	**Probability > F**
HabitatType Group	11	.0001	11	.4229
Cover Type	12	.7401	13	.0831
Habitat Type Group*Cover Type	34	.6126	45	.8361
Structure Class	3	.5985	3	.1442
Habitat Type Group*Structure Class	19	.0358	20	.3060
Cover Type*Structure Class	22	.5558	36	.5386

Habitat Group*Cover*Structure	17	.9070	42	.1532

Table 6.16: Results of analysis of variance using habitat type, forest type and structure class to predict root disease severity levels.

	M332a		M333d	
Factor	**Degrees of Freedom**	**Probability > F**	**Degrees of Freedom**	**Probability > F**
Habitat Type Group*	10	.0078	10	.0112
Forest Type	53	.0193	117	.0001
Habitat Type Group*Forest type	40	.2437	104	.3979
Structure Class	3	.0170	3	.0776
Habitat Type Group*Structure Class	20	.0993	19	.1943
Forest Type*Structure Class	40	.4521	98	.0050
Habitat Group*Forest*Structure	8	.5303	27	.1912

Habitat type groups

Root disease was particularly important in the habitat type groups with moderate levels of moisture and moderate to cold temperatures. In polygons with no sign of harvest activity in M332a, groups 3, 4, 5, and 7 all had particularly high proportions of polygons affected by root disease as well as higher than average levels of root disease severity overall (Figure 6.16). Among the unharvested polygons in M333d, groups 2, 3, 7 and 10 all had higher than average root disease severities (Table 6.17) although proportions of polygons affected by root disease varied more than that seen in M332a (Figures 6.16 and 6.17). The ranges in root disease severity were broad in all well-sampled habitat type groups with the highest levels of severity somewhat higher for most habitat type groups in M333d than in M332a. The lowest average disease severity among the well-sampled habitat type groups occurred, not surprisingly, in habitat type group 1. The dryness and, often, low stocking density of these sites probably contribute to low pathogen biomass and the frequent low-intensity fires that probably once typified disturbance these sites, would have limited pathogen biomass by favoring disease-resistant ponderosa pine. The 1935-era survey of the habitat type Group 1 sample polygons found 73 percent pine cover types and 9 percent recent burns (non-forested) in M332a, and 90 percent pine cover types in M333d.

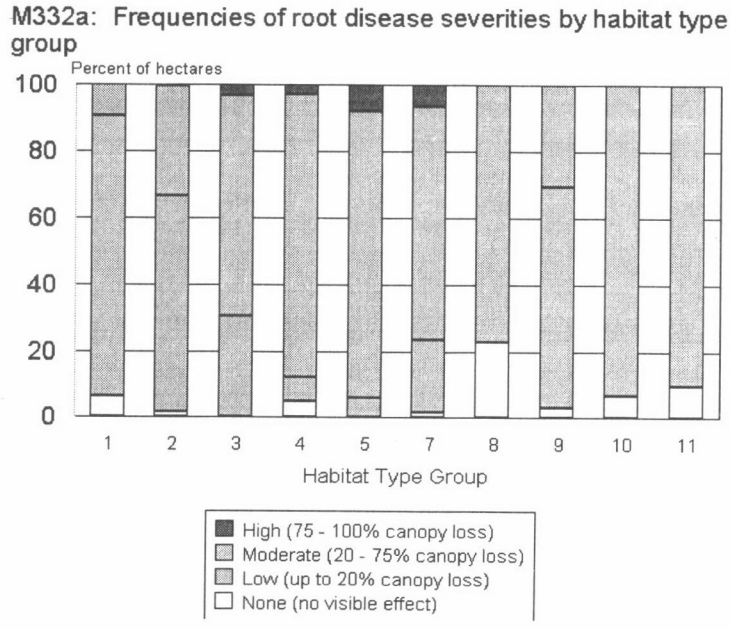

Figure 6.16: Frequency of root disease severity by habitat type in M332a.

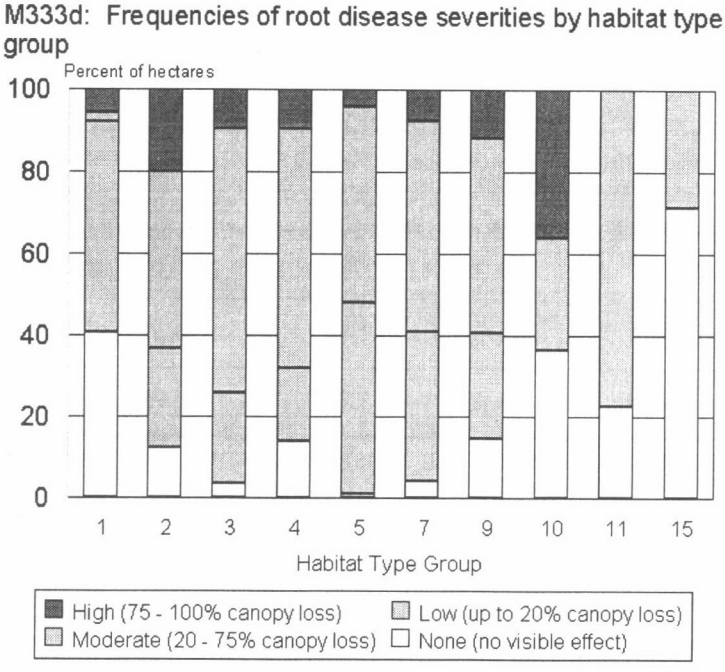

Figure 6.17: Frequency of root disease severity by habitat type in M333d.

Table 6.17: Consistency, range and average severity of root disease by habitat type group in polygons with no evidence of past harvest activity.

1975 era	M332a (6459.8 ha. with no harvest)			M333d (20,807.2 ha. with no harvest)		
Habitat Type Group	RRSV>0 Proportion of Polygons	Range RRSV	Average RRSV	RRSV>0 Proportion of Polygons	Range RRSV	Average RRSV
1	0.94	0 - 5	2.1	0.59	0 - 8	2.0
2	0.98	0 - 7	3.2	0.86	0 - 9	4.4
3	1.00	0 - 7	4.1	0.98	0 - 8	4.6
4	0.95	0 - 7	4.7	0.86	0 - 9	3.9
5	1.00	0 - 8	4.9	1.00	0 - 9	3.9
6*	1.00	3	3.0	1.00	2	2.0
7	0.98	0 - 7	4.6	0.97	0 - 9	4.2
8*	0.77	0	1.9	1.00	3	3.0
9	0.97	0 - 6	2.9	0.85	0 - 9	3.8
10	0.93*	0 - 3*	1.6*	0.63	0 - 9	4.0
11*	0.90	0 - 3	1.8	0.77	0 - 2	1.6
15*	1.00	2 - 3	2.4	0.31	0 - 5	1.5
ALL	0.97	0 - 8	3.7	0.94	0 - 9	4.0

*Sample sizes are small, so results are not considered indicative of these habitat types.

A surprising discovery of this analysis was the prevalence and severity of root disease in the cold habitat types, groups 7 and 9. Both the average disease severities and consistency were higher than expected in these habitat type groups. Subalpine fir is know to be very susceptible, particularly to annosus and Armillaria root diseases.

Cover types

The cover type associated with the highest average root disease severity in M332a was western redcedar/grand fir. This is not surprising as on cedar habitats, the progress of root disease often results in death of the Douglas-fir component first, followed by the grand fir component: western redcedar replaces the seral species as they die out. The root disease severity reaches it's maximum before the cover has converted to a majority of western redcedar. These

stands typically have very low remaining canopy density with abundant young cedar and grand fir in the understory.

In both ecosections, the western larch/Douglas-fir cover type had high average root disease severities. Low-intensity ground fires to mixed-severity fires probably had a historical role in maintaining the larch cover types. In the absence of fires during our analysis period (1935 era to 1975 era), root disease may have played an unusually important role in maintaining larch. Root disease probably reduced lateral competition from Douglas-fir, allowing for better survival of larch or reducing Douglas-fir stocking enough to allow the larch component to meet the 10 percent minimum component criterion (Table 6.18). In reality, it is very likely that root disease and fire have both been important factors in maintaining larch on these sites before effective fire suppression came into play because of the high average root disease severities in 1975-era polygons that were larch/Douglas-fir cover types in the 1935 era. From the larch/Douglas-fir cover type in the 1935 era, the average root disease severity in the 1975 era in M332a was 4.6 and in M333d, 4.3. In both cases very little of the area which had larch/Douglas-fir cover type in the 1935 era remained so in the 1975 era. Of 8 cover types derived from the 1935-era larch/Douglas-fir in M332a, only 2 percent was still larch/Douglas-fir in the 1975 era. The rest were predominantly subalpine fir and grand fir. In M333d, only 7 percent remained larch/Douglas-fir with subalpine fir, Douglas-fir and grand fir being the most common replacements.

Cover types with the lowest average root disease severities were ponderosa pine and nonforested in both ecosections and western redcedar in M333d. The reason for the difference in average disease severity in polygons with western redcedar cover types is not immediately obvious. In both cases the majority of hectares, 61 percent in M332a and 68 percent in M333d, assigned this cover type were also assigned the single-species cedar forest type. In both cases, the majority of sample polygons were in structure class 3, indicating that, superficially at least, they were in similar stages of succession. The disease severities in this cover type in M332a were nearly all high, with 71 percent of hectares assigned severity ratings of 4 or higher. Those in M333d were consistently low, ranging from 2.5 to 3.1. It is also possible that this apparent trend is an artifact of relatively small samples of only 250.4 hectares in M332a and only 361.6 hectares in M333d, in the 1975 era.

Table 6.18: Average root disease severity associated with major cover types represented in the 1935-era sample.

		M332a		M333d	
Description*	**Code**	**1935-era Hectares**	**RRSV Avg. 1975**	**1975-era Hectares**	**RRSV Avg. 1975**
White pine GE** 15%	1	441.5	3.7	7690.1	3.6
Ponderosa pine GE 80%	2.8	885.1	2.3	279.1	1.8
Ponderosa pine GE 25%	2	499.7	3.5	928.2	3.5
Western larch and Douglas-fir GE 75% with larch GE 10%	3	594.3	4.5	3580.1	4.7
Western hemlock and grand fir GE 50% (at least one live western hemlock)	4	0	NA	434.8	3.9
Douglas-fir GE 60%	5	885.9	3.4	1408.1	4.4
Engelmann spruce GE 50%	6	40.8	4.0	198.7	3.6
Lodgepole pine GE 50%	7	1347.6	2.9	1600.8	3.3
Western redcedar GE 50%	8	133.2	4.5	53.5	2.9
Western redcedar and grand fir GE 50% (at least one live cedar)	9	325.5	4.9	111.7	4.5
"Alpine"	11	728.5	3.8	1960.1	4.1
Non-forested because of site factors limiting tree survival	19, 23, 17, 18	245.1	2.1	127.9	2.1
Non-forested because of tree harvests	13,14	0	1.1	105.6	1.8
Non-forested because of wildfires	15,16	158.3	NA	3531.7	NA
Non-forested because of cultivation	21	0	0	20.2	0

* The cover types are listed in priority. Stands were assigned the first cover type for which they qualified. Percent compositions are by cubic foot volume in sawlog stands and live trees per acre in seedling to pole-size stands.

** GE = greater than or equal to

Structure classes

The average root disease severities in the 1975 era by structure class were all quite similar for structure classes 2, 3, and 4 within and between ecosections M332a and M333d (Table 6.19). For these structure classes, the average severities ranged from 3.3 in M332a structure class

(SC) 2, to 4.9 in M333d SC 3. The ranges in root disease severities were similar for all structure classes as well. The average severities for both ecosections were lower for SC 0 and 1 than in the larger-tree classes. This is probably, in part, because it is difficult to see the dead trees in the aerial photographs when the tree crowns are very small, so they may not accurately portray the relative biomass of pathogens on sites with these structure classes.

Table 6.19: Root disease severities by structure class.

	M332a (8,135-hectare Sample)		M333d (22,832.3-hectare Sample)	
Structure Class	Average RRSV	RRSV Range	Average RRSV	RRSV Range
0	2.5	0 - 8	2.1	0 - 6
1	2.8	0 - 8	3.0	0 - 9
2	3.3	0 - 7	4.0	0- 9
3	4.9	1 - 7	4.0	0 - 9
4	4.1	0 - 8	4.4	0 - 9

The presence of structure class 1 in the 1975-era sample could be attributed to regeneration following tree harvests, blister rust epidemics, and bark beetle outbreaks as well as severe root disease. So, in those stands which were initiated after recent harvests or other non-root disease disturbances, it is likely that lower average severities in SC 1 also resulted from root disease having had little time to develop.

In M332a, polygons in structure class 1 in the 1975 era that had no apparent harvest history were rated 0 - 8 for root disease severity, with an average of 2.8, and only 11 percent rated 0. Only four stands had been heavily harvested (essentially clearcut) and they were rated 0 to 3 for root disease severity. In the 69 hectares with moderate levels of harvest, the range in disease severity ratings was 2 - 6, with a weighted average of 3.6.

In M333d, the range in disease severity in the structure class 1 polygons with no evidence of harvest was 0 - 9, with 16 percent rated as 0. The average severity was 3.1. Moderate harvest was seen on only 14.6 hectares which were assigned a root disease severity range of 2 - 4, averaging 3.5. Heavy harvest was seen on 828.5 hectares with a root disease severity range of 0-9, 16 percent rated 0, and an average root disease severity of 2.7. The moderate levels of harvest may have been intentionally directed toward stands with higher initial root disease severity or they may have increased root disease severity, a consequence thought to be related to the stumps that serve as a food base for the fungi.

The combination of habitat type and structure class was significantly related to root disease severity of polygons in the 1975-era sample of M332a (Table 6.15). Tables 6.20 and 6.21 compare the major polygon classes present in the 1935-era sample to the root disease severity statistics related to those classes based on the 1975-era sample. Several of the major classes in the 1935 era had low average root disease severities and relatively low maximum disease severities. For example in both ecosections, habitat type group 1, structure class 4 the average root disease severity ratings were fairly low in the 1975 era with a maximum value of 5, which

probably indicates that polygons in this polygon class have a relatively low disease potential regardless of the point in time. Conversely, habitat group 5 in virtually any structure class, including very young classes had fairly high average severities. The maximum values were also very high indicating that some sites are likely to support heavy root pathogen biomasses. There were also some polygons in each structure class of habitat type group 5 rated '0', indicating minimal pathogen biomass.

Table 6.20: Major polygon classes in the 1935-era samples of M332a and their respective average root disease severities based on 1975-era API statistics.

M332a Major Polygon Classes in 1935-era			Statistics Based on 1975-era Sample		
Habitat Type Group	Structure Class	1935-era ha. (prop.)	RRSV Avg.	RRSV Range	1975-era Hectares
1	4	253.6 (.04)	2.1	0 - 5	225.6
2	2	241.1 (.04)	3.1	0 - 5	308.6
2	4	842.5 (.13)	3.6	0 - 7	794.3
3	2	236.3 (.04)	3.8	0 - 7	296.7
4	2	188.9 (.03)	4.7	4 - 6	96.3
4	4	113.4 (.02)	5.4	0 - 7	266.9
5	1	151.2 (.02)	5.1	1 - 8	155.3
5	2	427.3 (.07)	5.1	4 - 6	111.7
5	3	334.7 (.05)	4.7	1 -7	653.3
5	4	179.1 (.03)	5.0	3 -8	361.9
7	2	264.9 (.04)	4.2	0 - 7	217.1
7	4	169.5 (.03)	4.3	1 - 6	274.9
9	1	231.7 (.04)	1.8	0 - 6	59.6
9	2	1,010.2 (.16)	3.2	0 - 6	777.2
9	4	352.3 (.06)	2.6	1 -5	321.7

Table 6.21: Major polygon classes in the 1935-era samples of M333d and their respective average root disease severities based on 1975-era API statistics.

M333d Major Polygon Classes in the 1935 era			Statistics Based on 1975-era Sample		
Habitat Type Group	Structure Class	1935-era ha. (prop.)	RRSV Average	RRSV Range	1975 Hectares
2	1	810.4 (.04)	2.9	0 - 9	463.2
2	2	301.1 (.01)	3.2	0 - 9	1,153.1
2	4	624.6 (.03)	3.6	0 - 9	580.6
3	1	255.7 (.01)	4.0	0 - 8	43.5
3	4	207.3 (.01)	3.8	0 - 6	46.5
4	1	592.5 (.03)	2.0	0 - 7	275.3
4	2	551.3 (.03)	4.8	0 - 7	897.2
4	4	717.5 (.03)	4.5	0 - 9	901.6
5	1	2,540.6 (.12)	3.7	0- 7	1,229.2
5	2	1,807.1 (.08)	5.1	2 - 9	3,846.7
5	3	1,114.5 (.05)	3.4	0 - 7	3,468.7
5	4	3,419.4 (.16)	4.3	2 - 9	1,930.0
7	1	769.9 (.03)	2.8	0 - 7	455.1
7	2	661.5 (.03)	3.3	0 - 9	1,284.0
7	4	1,280.6 (.06)	4.3	0 - 8	592.2
9	1	565.1 (.03)	4.2	0 - 9	779.4
9	2	367.2 (.02)	4.1	0 - 9	1,594.4
9	4	575.5 (.03)	5.0	0 - 8	275.3

Sources of Root Disease Severity Levels in the 1975 Era

Ecosection M332a

The combined influence of habitat type and cover type on the development of severe root disease can been seen in the trends from the 1935 era to the 1975 era (Table 6.22). Cover types that are expected to support large biomasses of root pathogens, those that have a high proportion of preferred hosts, generally lead to polygons with significantly higher root disease severities at the end of the 40-year period than did those that started with root disease-resistant cover types. Ponderosa pine and lodgepole pine generally had low root disease severities at the end of the 40-year period. Likewise, polygons that were non-forested in the 1935 era tended to have low severities in the 1975 era, with the exception of habitat type group 5. Polygons that had been assigned "alpine" cover type in the 1935 era also tended to have low 1975-era severities. Most of this type occurred in habitat type groups 7 and 9. Habitat type group 7, in particular, varied greatly in disease severity depending on the 1935-era cover type. Western white pine and larch/Douglas-fir cover types both lead to high average root disease severities on sites in this habitat type group.

Table 6.22: M332a: The relationship between initial cover type and root disease severity 40 years later. Shown is the average root disease severity of polygons in the 1975 era grouped by their 1935-era cover types. Cover type/habitat type group classes represented by at least 70 hectares in the 1935-era survey are presented.

Cover Type	Habitat Type Groups									
Code	All	1	2	3	4	5	7	8	9	10
2	2.3	1.3	2.2					2.6		
11	2.4						3.4		2.2	1.9
15 and 16	2.7		2.4			4.7	2.2		2.0	
2.8	2.7	2.5	2.7						2.9	
7	3.3			3.9		3.9	3.6		3.3	2.0
5	3.8		3.3			5.6	2.6		2.6	
6	4.0					4.7	3.9		3.7	
1	4.3				4.5	4.6	5.0		3.2	
3	4.4			4.0	4.2	4.8	5.1			
8	4.7					4.3				
9	4.8					5.0				

Ecosection M333d

Ponderosa pine and lodgepole pine cover types had the lowest disease severities 40 years later, regardless of their ending cover types (Table 6.23). Recent and older burns which hadn't reforested in 1935 era had fairly high average root disease severities 40 years later considering how young the stands were in the 1975 era. Grand fir, white pine, subalpine fir, ponderosa pine mixed with Douglas-fir and Douglas-fir cover types from 1935 era were similarly high in severity after 40 years. It was somewhat surprising that the highest average severities in the 1975 era came from 1935-era western larch/Douglas-fir mixed type and western hemlock/grand fir mixed type.

The high level of disease severity resulting from 1935-era white pine stands has been examined in a number of recent reports (Byler and others 1994, Monnig and Byler 1992). Part of this outcome is likely to a disturbance-response mechanism as explained by Wargo (1995) wherein the exotic pathogen, white pine blister rust, caused a disturbance. This resulted in a response in which tree species composition was shifted to other, more root disease-susceptible species (primarily Douglas-fir, grand fir and subalpine fir). Root pathogens then responded by increasing in proportion to the availability of the preferred hosts.

Table 6.23: M333d: The relationship between initial cover type and root disease severity 40 years later. Shown is the average root disease severity of polygons in the 1975 era grouped by their 1935-era cover type. Cover type/habitat type group classes represented by at least 100 hectares in the 1935-era survey are presented.

Cover Type	Habitat Type Groups					
Code	All	2	3	5	7	9
2.8	1.7	0.6				
7	2.6	3.1		2.8	2.5	2.3
15 and 16	3.3	3.7	4.0	4.2	2.6	2.4
6	3.4				3.5	
9	3.5					
1	3.6	2.9	3.3	3.6	3.5	3.5
11	3.7			4.7	3.9	3.7
2	3.8	4.0	2.4	5.5		
5	3.9	3.3	4.3	3.6		6.1
3	4.3		5.0	4.2	4.3	4.5
4	4.8			4.6	5.0	

Succession influence

The relative influence of root disease on succession generally corresponded to the disease severity level. The root disease severity levels generally were higher in M332a than in M333d. This is probably, at least in part, due to the more advanced age of stands in M332a overall. The overall average age (weighted by hectares) of stands in the 1975 era in M332a was 87 years, compared to 72 years in M333d. Root disease severity typically increases with age in a susceptible stand so the stands in M332a have had roughly 15 more years of cumulative root disease effects than those in M333d. The ameliorating effects of species mixtures are evident in the relationships between root disease severity and succession influence on habitat types which support a large number of tree species compared to those which support few. The average difference between root disease severity and level of succession influence was very small in

Forest type was significantly associated with root disease severity and subsequent influences on succession. The highest average root disease severity was seen in forest types that included cedar, grand fir, Douglas-fir and western white pine (Table 6.24).

Table 6.24: Average root disease severity and succession influence of root diseases by forest type components.

	M332a			M333d		
Forest Type Component	**1935-era (6,286 Hectares)**	**Average 1935-era RRSV**	**Average Succession Influence**	**1935-era (22,003 Hectares)**	**Average 1935-era RRSV**	**Average Succession Influence**
Western redcedar	598	4.9	M	555	4.3	L-M
Grand fir	916	4.6	M-H	3,117	4.1	M-H
Douglas-fir	2,633	3.4	M-H	6,072	4.2	M-H
Western white pine	441	4.1	M-H	6,581	4.9	M
Western larch	2,295	3.4	M	7,063	3.2	M
Ponderosa pine	1425	2.1	M	1,652	3.2	M
Lodgepole pine	2,067	3.2	L-M	3,175	2.9	L-M
Subalpine fir	1,523	3.0	M-H	1,044	4.0	M-H
Non-forested	654	2.3	M	4,265	2.4	L-M
Whitebark pine*	176	2.5	L	36	4.4	L

* The sample size for whitebark pine is too small to confer significance to these data.

Succession functions of root pathogens

Several significant succession functions were common to most habitat type groups. The most severe effects from root disease results in suspending changes in structure class in a small, relatively young tree class: e.g., seedling/sapling or pole. Severe root disease may also move a stand from a structure typified by large trees to one with few large trees. The latter function is seen in transitions from structure class 3 (mature, closed canopy) to structure class 2 or 1, or from 4 to 2 or 1. Both of these functions are manifest on sites as root disease patches. There typically is abundant regeneration in a patch, though not always so. Suspended or regressing succession was seen on 30 percent and 32 percent of hectares in M332a and M333d, respectively. High or moderate root disease influence was seen in 81 percent of these hectares for each of the ecosections. White pine blister rust, alone and functioning in combination with root disease, and mountain pine beetle in lodgepole pine accounted for the remaining stalled or regressing polygons. Decreasing density in large-tree stands or preventing canopy closure in stands which are progressing from seedling/sapling or pole classes to large-tree stands, were also common functions of root pathogens. Also important, although harder to discern from silvical succession, is pushing the species composition toward the "climax" tree species. This function was seen on 51 percent and 69 percent of hectares in M332a and M333d, respectively, where root disease influence was evident. It generally occurred in conjunction with stalling or moving backward in structure classes or preventing canopy closure.

Taken in combination, the cover type and structure effects of root pathogens could be categorized into 28 successional effects (Table 6.25). There were sizable difference between the two ecosections in the importance of each potential type of successional effect. Most common in ecosection M332a was a stable structure between the 1935-era survey and the 1975-era resurvey. In this case the stands were in a mature structure class with canopy densities indicative of fairly complete site occupation. On more productive sites, this is seen in polygons found to be in structure class 3 at both the initial survey and 40 years later, in the resurvey. Similarly, on higher elevation sites, polygons were seen to remain in structure classes 2 or 4, and on harsh, dry sites, they remained in structure class 4. Each of these situations was interpreted to indicate a stable structure. In M332a, stable structures were about evenly split among unchanging cover type, increased climax components, and maintenance of early seral components. In contrast, M333d stable structures were relatively uncommon. The most important influence of root pathogens in this ecosection was to suspend structures in young, small tree classes. This was generally in combination with increases in late seral or climax tree species or maintaining early tree species. The cover type remained similar over the 40-year period on very few hectares in M333d.

Table 6.25: Successional effect of root pathogens based on changes in cover type and structure class of polygons affected by root disease from the 1935 era to the 1975 era.

Structure Change	Cover Change	Ecosection M332a		Ecosection M333d	
		Hectares	Prop.	Hectares	Prop.
Structure stable (no change)	No change in cover type	1686.3	0.36	1219	0.07
	Increase climax components		.29		.42
	Maintain early seral components		.25		.46
	Increase relative proportion of early seral components		.09		.05
Normal change to larger trees with moderate to high canopy density	Increase climax components	1,036	.58	4,596	.64
	Maintain early seral components		.22		.26
	No change in cover type		.20		.05
	Increase relative proportion of early seral components		.00		.05
Stand closure prevented (low canopy density results)	Increase climax components	856	.58	3,508	.63
	No change in cover type		.23		.10
	Maintain early seral components		.15		.19
	Increase relative proportion of early seral components		.04		.07
Structure stalled in young, small tree class	Increase climax components	708	.58	6,061	.50
	Maintain early seral components		.21		.44
	No change in cover type		.20		.05

	Increase relative proportion of early seral components		.01		.02
Largest trees die; move toward young, small-tree classes	Increase climax components	684	.71	3,616	.46
	Maintain early seral components		.20		.21
	Increase relative proportion of early seral components		.07		.08
	No change in cover type		.03		.24
Large-tree structure; increase in canopy density	Increase climax components	440	.66	2,722	.52
	Increase relative proportion of early seral components		.15		.06
	No change in cover type		.13		.16
	Maintain early seral components		.06		.26
Large-tree structure; decrease in canopy density	No change in cover type	116	.35	282	.00
	Maintain early seral components		.28		.11
	Increase climax components		.19		.89
	Increase relative proportion of early seral components		.17		.00

Succession Regimes of Root Pathogens

Although the succession functions are observed over a relatively short period of time (40 years or less), when considered as segments of a cycle or extended timeline (thousands of years in duration), they can be pieced together into successional regimes. In constructing these probable scenarios, it is important to bear in mind that root pathogens are slow to change in location and biomass, so that they are unusually stable influences compared to other biological agents such as bark beetles, defoliating fungi or insects, browsing herbivores, and so on.

Warm to moderately warm and dry habitat types (Groups 1 and 2)

The most common regime on Douglas-fir and the few grand fir habitat types within these groups is typified by discontinuous distribution of root pathogen colonies. Colony biomass

increases and decreases in response to the species composition and density of the trees. At any one time, a part of the area will have sufficient stocking of Douglas-fir (or grand fir) for the fungus biomass to build and root disease patches to develop. Patches are discrete and generally less than 1 acre in size, although they can be much larger. Individual patches are probably have little pathogen genetic variability within species, indicating that they are derived from one or few spores. *Armillaria ostoyae* is often the most readily observed root pathogen on these sites. Establishment of new clones is infrequent due to the limited availability of suitable substrates and other environmental conditions. Conditions for expansion of established colonies also are seldom favorable for extended periods (more than one generation of trees), so colony convergence is not a major feature of this regime. Through time, the patches will increase somewhat while conditions are favorable. Fire intervals will greatly influence the ability of the fungal colonies to grow, although fire does not kill much of the fungus directly. Frequent ground fires favor seral ponderosa pine and open spacing: both of these conditions will tend to minimize the extent of root pathogens. It is probably relatively rare for a clone to die out completely, although an individual clone may become fragmented by extended periods of pine-dominated cover and discontinuous root distribution. When ecosections of the landscape periodically escape fire for long enough intervals to convert to a majority of Douglas-fir and sufficient stocking for root closure to occur, the colonies will increase in biomass. The change in both tree species composition and fungal colony biomass are not really cyclic: they are dependent upon the combination of fire return intervals (which are in part subject to chance), available moisture at the time of regeneration and the relative abundance of seed of ponderosa pine and Douglas-fir. Changes in both tree species composition and fungus biomass from one generation of trees to another are not likely to be wholesale but somewhat gradual under natural conditions.

Statistics from M332a for habitat type groups 1 and 2 (see Appendix A, Figures 1-3). The average root disease severity in habitat type group 2 in the 1975-era polygon sample was 3.1 with a range of 0 to 7. The predicted severity for the 1935-era polygon sample was lower, 1.9, resulting primarily from the lower proportions of Douglas-fir cover types in 1935 era. Root disease influence was seen in 87 percent of pathways in habitat type group 2 from the 1935 era to 1975 era. The relative influence of root disease in determining the transitions was high in 24 percent of the pathways but these pathways occurred on only 15 percent of the hectares in habitat type group 2. Moderate levels of influence was seen in 45 percent of pathways and 49 percent of the hectares in this habitat type group.

In both high and moderate levels of root disease influence, the pathways are essentially driven by root disease. This is particularly evident in the structural changes. On 47 percent of hectares where transitions were highly influenced by root disease, succession was either stalled in an early structure class (seedling/sapling or pole) or moved back toward smaller-tree-dominated stands (Table 6.26). These functions occurred on 24 percent of the hectares in habitat type group 2 that had moderate to high levels of root disease influence. Where structure was stalled, over 40 percent of hectares converted to later seral species, with only 3 percent remaining early seral species (Figure 6.20). On an additional 38 percent of the root disease-influenced hectares, canopy closure was prevented and densities and tree volumes were kept low (Figure 6.21). These are typical influences of root disease as disease patches form and spread. Although the seral pine components of stands in these HT groups would be favored by *Armillaria* root disease killing Douglas-fir, the function identified as maintaining the seral component was not as prevalent in the sample (26 percent) compared to conversion to more climax species

compositions (62 percent). This could be in part due to *Heterobasidion annosum* root disease in ponderosa pine (p-type), but it is more likely a result of mountain pine beetle activity in ponderosa pine. Most polygons that had mixed Douglas-fir and ponderosa pine and high to moderate root disease influence, also had high mountain pine beetle influences. The combined effect was to maintain the species mix or move the composition toward Douglas-fir while pushing the structure class back to smaller trees.

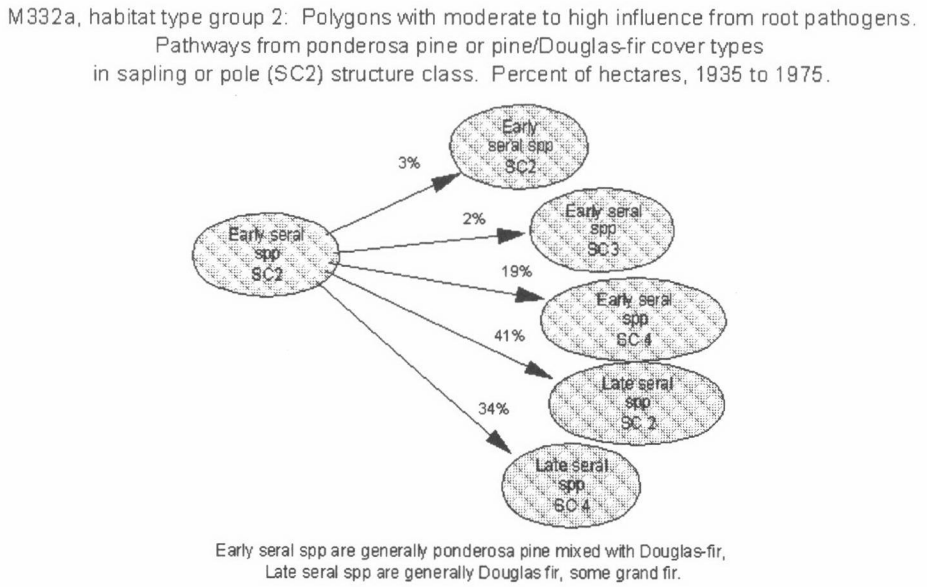
M332a, habitat type group 2: Polygons with moderate to high influence from root pathogens.
Pathways from ponderosa pine or pine/Douglas-fir cover types
in sapling or pole (SC2) structure class. Percent of hectares, 1935 to 1975.
Early seral spp SC2
3%
Early seral spp SC2
2%
Early seral spp SC3
19%
Early seral spp SC4
41%
Late seral spp SC 2
34%
Late seral spp SC 4
Early seral spp are generally ponderosa pine mixed with Douglas-fir,
Late seral spp are generally Douglas fir, some grand fir.

Figure 6.20: Pathways, ponderosa pine or pine/Douglas-fir cover types in structure class 2, habitat type group 2, moderate to high root pathogen influence, M332a.

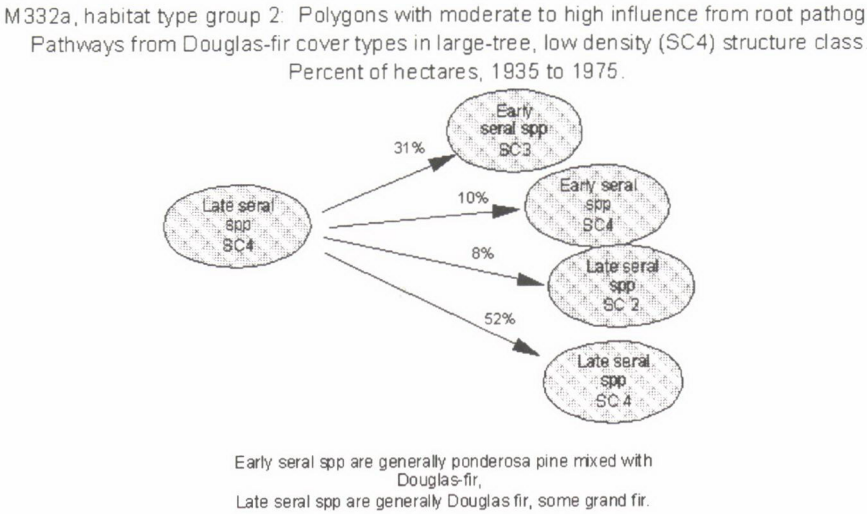
M332a, habitat type group 2: Polygons with moderate to high influence from root pathogens.
Pathways from Douglas-fir cover types in large-tree, low density (SC4) structure class.
Percent of hectares, 1935 to 1975.
Late seral spp SC4
31%
Early seral spp SC3
10%
Early seral spp SC4
8%
Late seral spp SC 2
52%
Late seral spp SC 4
Early seral spp are generally ponderosa pine mixed with Douglas-fir,
Late seral spp are generally Douglas fir, some grand fir.

Figure 6.21: Pathways, Douglas-fir cover types in structure class 4, habitat type group 2, moderate to high root pathogen influence, M332a.

Table 6.26: Cover and structure change functions of root pathogens in polygons classes with an average initial root disease severity greater than 0. The next 40 years is based on changes by polygon class remaining similar to those observed from the 1935 era to the 1975 era.

Habitat Type Groups 1 and 2	M332a		M333d	
	1935-1975	Next 40 years	1935-1975	Next 40 years
Cover change function				
Increase climax components	.61	.30	.56	.43
Maintain early seral components	.28	.35	.37	.29
Increase relative proportion of early seral components	.05	.19	.05	.10
No change in cover type	.06	.15	.03	.19
Structure change function				
Structure stable (no change)	.02	.01	00	00
Normal change to larger trees with moderate to high canopy density	.02	.02	.12	.03
Large-tree structure; increase in canopy density	.20	.10	.04	.04

Stand closure prevented (low canopy density results)	.46	.46	.23	.24
Largest trees die; move toward young, small-tree classes	.19	.14	.20	.12
Structure stalled in young, small-tree class	.08	.11	.41	.52

The influence of the 1935-era cover type on root disease development was evident in the 1975-era root disease severities in habitat type group 2. The most important cover types from the 1935-era survey were non-forested (recent burns, primarily), ponderosa pine, ponderosa pine/Douglas-fir mixture, and Douglas-fir. The average root disease severity in the 1975 era for polygons that had nearly pure ponderosa pine (greater than 80 percent) in the 1935 era was low, only 1.7. For those starting with a mixture of ponderosa pine and Douglas-fir, the severity in the 1975 era averaged 2.2, and for those starting with Douglas-fir cover in the 1935 era, it was 3.3.

The habitat type group 1 sample was small and the influence of root disease in this limited sample was comparable to habitat type group 2. Root disease severity averaged 2.1, and ranged from 0 to 5 in the 1975 era polygon sample (8,134 hectares). The average calculated severity for the 1935-era polygon sample was also 2.1. Although 70 percent of hectares had some level of root disease influence in succession, only 29 percent and 5 percent had moderate and high effects, respectively. A low level of root disease influence was most common, occurring on 35 percent of hectares. The association seen between root disease and mountain pine beetle in habitat type group 2 was not as apparent in habitat type group 1 although the outcome where it did occur was similar to that seen in habitat type group 2. Table 6.27 compares the relative influence of root disease on structure in habitat type groups 1 and 2 combined. There is relatively little regression in structure, changing from large tree classes to small tree classes, in the absence of significant root disease influence (moderate to high influence levels). Pathways with moderate to high root disease influences generally result in structures stalled in early stages (1 or 2) or often regressing from 3 or 4 to 1 or 2.

Table 6.27: Structure effects of root disease in habitat type groups 1 and 2 combined. Proportion of each 1935-era (start) structure class by their 1975-era (end) structure classes; comparing hectares with significant root disease influence to those without root disease influence. (The total of proportions for each starting structure class within each disease influence level for each ecosection will equal 1.00.)

Structure Class		M332a		M333d	
Start	End	RR influence Moderate or High	No RR Influence	RR influence Moderate or High	No RR Influence
0	0	0.0	0.0	0.1	>.1
0	1	0.1	-	0.7*	>.1
0	2	-	-	0.2*	0.9
0	3	0.2*	0.9		
0	4	0.7*	0.1	>.1	0.1
1	1	1.0	-	0.1	>.1
1	2	-	-	0.6	0.6
1	3	-	0.8	>.1	0.1
1	4	-	0.2	0.2	0.3
2	1	>.1	-	>.1	>.1
2	2	0.3	-	0.5	0.6
2	3	0.1*	1.0		
2	4	0.5	-	0.4	0.4
3	1	0.1	0.3	1.0	-
3	2	0.3	-		
3	3	0.2	0.5		
3	4	0.5	0.2		
4	0	>0.1	0.1	>.1	>.1

4	1	0.2	-	0.2	>.1
4	2	0.1	0.3	0.4*	>.1
4	3	0.1*	0.6	>.1*	1.0
4	4	0.6*	>0.1	0.4	>.1

*Proportion of hectares with this outcome are significantly different when influenced by root disease compared to those without root disease influence.

Statistics from M333d for habitat type groups 1 and 2 (see Appendix A, Figures 4-7). Root disease severity in habitat type groups 1 and 2 were 1.4 and 3.4, respectively in the 1975-era polygon sample. These are not significantly different from the predicted average severities for these habitat type groups in the 1935-era polygon sample (2.1 and 3.3 for habitat type groups 1 and 2, respectively). Root disease severities ranged from 0 to 8 in the 1975-era sample.

Root disease had a strong influence on succession. Root disease influence was seen in 82 percent of the pathways and 83 percent of the hectares, respectively, in habitat type groups 1 and 2. Root pathogens were the primary successional influence on 44 percent of hectares in the two groups. Moderate root disease influence was seen on an additional 27 percent of hectares. Stalling in an early structure class or moving back toward an earlier class (smaller trees overall) were the dominant influences (Figure 6.22), occurring on an amazing, 61 percent of hectares (Table 6.26). Such functions can be recognized as root disease patches that were typically well-stocked with young trees but failed to progress to larger trees over the 40-year period analyzed.

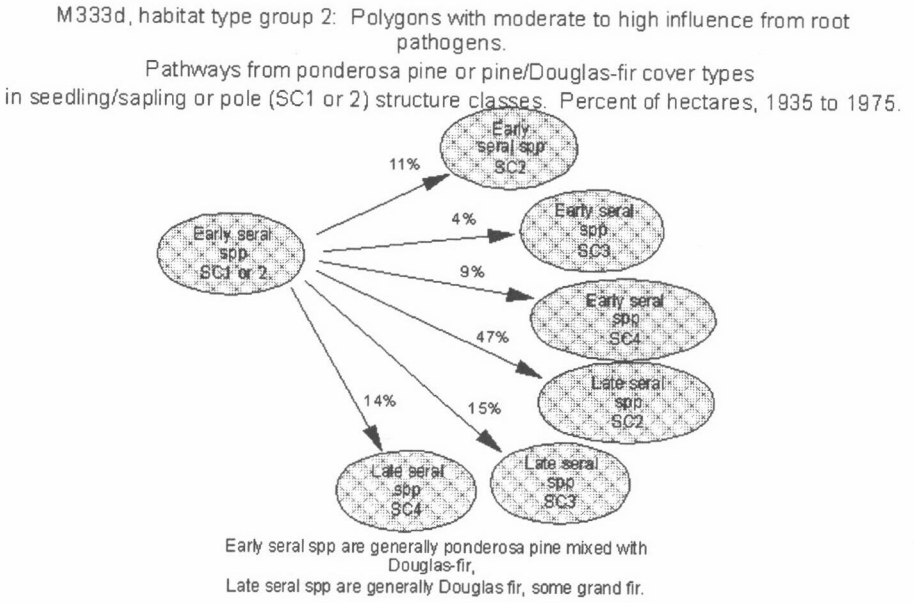
M333d, habitat type group 2: Polygons with moderate to high influence from root pathogens.
Pathways from ponderosa pine or pine/Douglas-fir cover types
in seedling/sapling or pole (SC1 or 2) structure classes. Percent of hectares, 1935 to 1975.
Early seral spp SC1 or 2
11%
Early seral spp SC2
4%
Early seral spp SC3
9%
Early seral spp SC4
47%
Late seral spp SC2
14%
15%
Late seral spp SC4
Late seral spp SC3
Early seral spp are generally ponderosa pine mixed with Douglas-fir,
Late seral spp are generally Douglas fir, some grand fir.

Figure 6.22: Pathways, ponderosa pine or pine/Douglas-fir cover types in structure classes 1 and 2, habitat type group 2, moderate to high root pathogen influence, M333d.

Canopy closure was prevented by root disease and, in some cases Douglas-fir beetle in a weeding type of function on 24 percent of hectares in these habitat type groups. In many cases the polygons which began in an open canopy condition (SC 4) in the 1935 era, regressed to an earlier structure class (SC 1 or SC 2) by the 1975 era. It is likely that many of those polygons which reached SC 4 by the 1975 era have or will regress to earlier structure classes as well. If patterns of change from the 1975-era polygon classes are similar to those from 1935 to 1975 eras, it would appear that about half of the 1975-era hectares in SC 4 will move backward to SC 1 or 2 by 2015 (Table 6.26). With such heavy influences from root disease, it is reasonable to expect SC 2, in particular to become a "collection class", one in which there are usually net gains through time in the absence of fires or direct management. This is evident in the relatively high proportions from each of the 1935-era structure classes which were in structure class 2 by the 1975 era with significant root disease influence and the indicated increase to 52 percent of hectares expected to be stalled in SC 1 and 2 between 1975 and 2015.

In contrast to M332a, increasing or maintaining the seral components was an important function in root disease-influenced polygons of habitat type groups 1 and 2 in M333d. Thirty-seven percent of hectares supported this function. This is likely due to relatively little influence of mountain pine beetle in the ponderosa pine in M333d. Ponderosa pine was maintained or increased in many polygons where Douglas-fir was killed by root disease and Douglas-fir beetle.

Trends in the subset of polygons present in 1935-era and 1975-era surveys

Trends in root disease severity for polygons in habitat type group 2 that were surveyed both in the 1935 and 1975 eras indicate a general trend toward higher severity classes and away from the low severity classes. When these polygons are projected forward, this trend appears likely to continue through 2015 (Table 6.28). The small sample size in M332a makes interpretation of these data difficult. However in M333d there is an distinct increase in the polygon classes that have the highest average root disease severities, RRSV classes 7 through 9. From essentially none in the 1935 era, the proportion increased to .13 by the 1975-era survey and is projected to increase to .16 by the 2015 era. Polygons in these severity classes have less than 25 percent of the level of canopy closure that would be considered normal for stands not afflicted by root disease.

Table 6.28: Distribution of root disease severity averages for polygon classes represented in the 1935 era (calculated based on actual polygon class), 1975 era (measured), and 2015 (calculated based on projected outcome). Proportions of hectares in the subasample.

	M332a (725-hectare subsample)			M333d (2197.7-hectare subsample)		
RRSV	1935	1975	2015	1935	1975	2015
0	.08	.23	.08	.14	.00	.00
1	.28	.01	>.01	.21	.12	.10
2	.03	.39	.19	.16	.15	.09
3	.38	.22	.40	.25	.14	.22

4	.23	.09	.16	.06	.22	.10
5	.00	.05	.17	.01	.16	.28
6	.00	.00	.00	.17	.09	.05
7	.00	.00	.00	.00	.09	.15
8	.00	.00	.00	.00	.02	.01
9	.00	.00	.00	.00	.01	>.01

The 1935-era cover type had a fairly modest influence on the corresponding root disease severity in these polygons in the 1975 era. Of several important cover types in habitat type group 2 in the 1935 era, mixtures of ponderosa pine or western larch with Douglas-fir produce the highest severities, (3.9 and 3.8, respectively) in the 1975 era (Table 6.29). Western white pine and ponderosa pine cover types lead to the lowest root disease severities, 2.9 and .6, respectively. These data also demonstrate the ability of root pathogens to withstand the effects of wildfire. The average 1975-era root disease severity on sites that coded as recently burned in 1935 era was the same as the average for the unburned polygons.

Table 6.29: M333d: important 1935-era cover types of polygons habitat type group 2 and the average root disease severity of the polygons after 40 years.

M333d: 1935-era Cover Type	1975-era Root Disease Severity
Ponderosa pine/Douglas-fir mixture	3.9
Western larch mixtures	3.8
Non-forested (mostly recent burns)	3.7
Douglas-fir	3.3
Lodgepole pine	3.1
Western white pine	2.9
Ponderosa pine	0.6

Moderately warm and moderately dry habitat types, Group 3. On the grand fir habitat types in this group, Douglas-fir and ponderosa pine are the major seral species. On the Douglas-fir habitat type (*Pseudotsuga menziesii/Linnaea borealis),* Douglas-fir and ponderosa pine are the most prevalent components. In either case, root pathogens have a nearly continuous supply of preferred hosts so they are able to colonize most of the area occupied by these habitat types. Individual colonies of any one pathogen species will merge to give the appearance of extensive single colonies. *Armillaria ostoyae* is particularly common on these sites. Studies of

naturally occurring *Armillaria bulbosa* colonies have shown minimal overlap of individual clones of the species indicating that they are capable of excluding other individuals of the same species (Smith et al. 1992). They do not, however, exclude other species of root pathogens, so multiple pathogens commonly appear on a single site.

Over generations of trees, the fungus clones are likely to be fragmented by occasional discontinuity in susceptible root tissues on the site. Changes in species composition and density over the generations on a site will influence the biomass of root pathogens. After ponderosa pines have dominated a site for at least a generation, if fire intervals become conducive to Douglas-fir survival for a period, the pathogen biomass may be low enough for a fairly dense forest dominated by Douglas-fir to develop. Grand fir is somewhat more resistant to the major root pathogens on these habitat types and will maintain more of presence in a maturing forest than will Douglas-fir where pathogen biomass is significant.

Current experience with conversion of these sites to greater proportions of Douglas-fir and grand fir by fire exclusion and selective harvest indicates that a single generation dominated by these tree species is probably all that is needed to establish nearly continuous pathogen colony coverage of sites. The result is that, as forests of this composition reach maturity and colony biomass nears maximum, mortality rates of Douglas-fir and grand fir will approach epidemic levels. Large, open root disease patches develop, with extremely low canopy densities. These patches are typically occupied to various degrees by Douglas-fir and grand fir seedlings and saplings, brush, forbs and grasses. Between the patches the fungus biomass would be lower and canopy densities higher.

In the continued absence of fire the patches converge and mortality in intervening areas would produce root disease patches over increasingly large areas. The return of crown fire may incrementally increase the amounts of ponderosa pine on these sites but it is unlikely that changes in species composition would be rapid over large areas of these habitat types. At any one time, considerable areas of this habitat type may have large open patches of root disease that are maintained for one to several generations with high fungus biomass.

Statistics from M333d and M332a (see Appendix A, Figures 8-9). This habitat type group is relatively poorly represented in these ecosections. Of the 597 hectares in this habitat type group in M333d, 95 percent had some level of root disease succession influence; 56 percent had moderate to high levels of influence. In M332a, 71 percent had some root disease succession influence and 70 percent was either high or moderate influence. The consistent presence of root disease in this habitat type group is also evident in the low proportion of hectares in our sample that were assigned a root disease severity level of zero (5 percent in M333d and less than 1 percent in M332a).

In both ecosections, the primary function of root disease was to stall the structure in seedling, sapling, or pole-size classes (Figure 6.23).This function was seen on 60 percent of hectares in both M333d and M332a where root disease severity was greater than 0. With this type of structure change, there were roughly equal probabilities of pushing composition toward late-seral species (generally grand fir) and increasing or maintaining early seral pines. Preventing canopy closure in large-tree structure classes was not an important root disease function in M333d but was seen in 39 percent of root disease-influenced hectares in M332a.

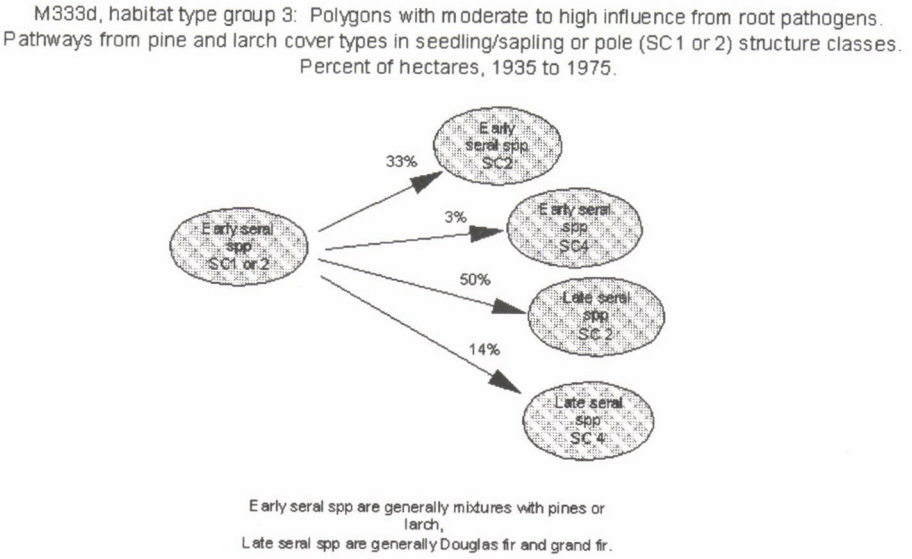
M333d, habitat type group 3: Polygons with moderate to high influence from root pathogens.
Pathways from pine and larch cover types in seedling/sapling or pole (SC1 or 2) structure classes.
Percent of hectares, 1935 to 1975.
Early seral spp SC1 or 2
33%
Early seral spp SC2
3%
Early seral spp SC4
50%
Late seral spp SC 2
14%
Late seral spp SC 4
Early seral spp are generally mixtures with pines or larch,
Late seral spp are generally Douglas fir and grand fir.

Figure 6.23: Pathways, pine and larch cover types in structure classes 1 and 2, habitat type group 3, moderate to high root pathogen influence, M333d.

Moderately warm and moist habitat types, Group 4 (see Appendix A, Figures 10-17). At the moister end of the grand fir habitat type series western larch and western white pine dominate a proportion of the sites. They, like ponderosa pine and lodgepole pine, require crown and/or ground fires to maintain their competitive edge. Douglas-fir and grand fir are both important components of most stands, at least initially. But with the greater species mixture compared to the drier types, the omnipresent root pathogens will tend to remove Douglas-fir and grand fir from the mixed stands, thereby thinning the stands and further favoring the larch and pines. In the M332a sample of habitat type group 4, root disease functioned to retain seral species on 12 percent of hectares. In M333d, root disease helped retain serals on 27 percent of hectares. This function was particularly evident in stands in M333d that were seeling/sapling or pole-size in the 1935 era. Figure 6.24 illustrates the change for early seral species; Figure 6.25 illustrates the change for mid-seral species.

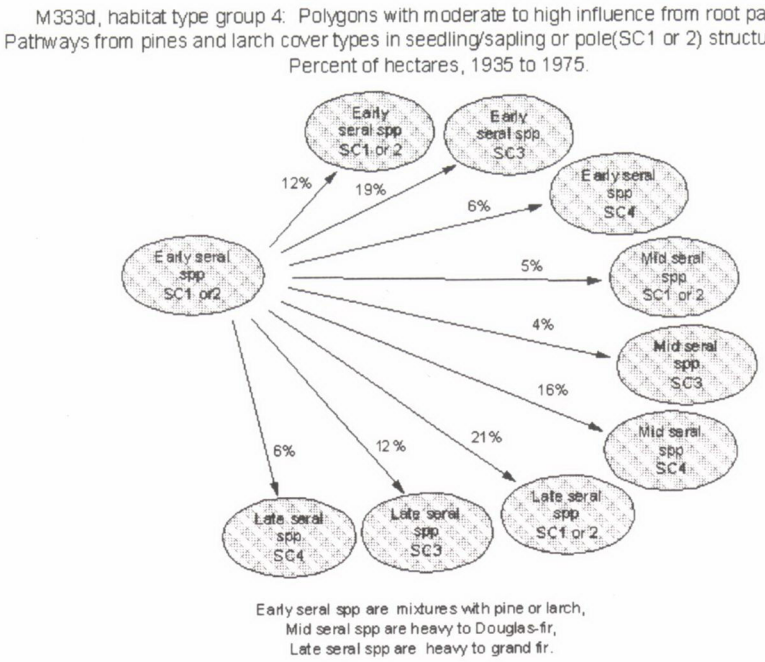
M333d, habitat type group 4: Polygons with moderate to high influence from root pathogens.
Pathways from pines and larch cover types in seedling/sapling or pole(SC1 or 2) structure classes.
Percent of hectares, 1935 to 1975.
Early seral spp SC1 or 2
Early seral spp SC3
Early seral spp SC4
Mid seral spp SC1 or 2
Mid seral spp SC3
Mid seral spp SC4
Late seral spp SC1 or 2
Late seral spp SC3
Late seral spp SC4
12%
19%
6%
5%
4%
16%
21%
12 %
6%
Early seral spp are mixtures with pine or larch,
Mid seral spp are heavy to Douglas-fir,
Late seral spp are heavy to grand fir.

Figure 6.24: Pathways, pine and larch cover types in early seral stage, structure classes 1 and 2, habitat type group 4, moderate to high root pathogen influence, M333d.

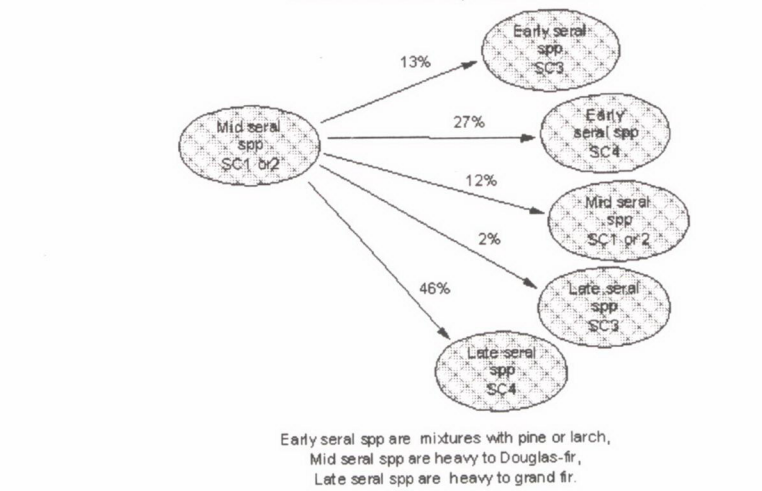
M333d, habitat type group 4: Polygons with moderate to high influence from root pathogens.
Pathways from pines and larch cover types in seedling/sapling or pole(SC1 or 2) structure classes.
Percent of hectares, 1935 to 1975.
Early seral spp SC3
Early seral spp SC4
Mid seral spp SC1 or2
Mid seral spp SC1 or2
Late seral spp SC3
Late seral spp SC4
13%
27%
12%
2%
46%
Early seral spp are mixtures with pine or larch,
Mid seral spp are heavy to Douglas-fir,
Late seral spp are heavy to grand fir.

Figure 6.25: Pathways, pine and larch cover types in mid-seral stage, structure classes 1 and 2, habitat type group 4, moderate to high root pathogen influence, M333d.

The occurrence of patches of root disease depends upon the occurrence of patches of forest dominated by Douglas-fir or grand fir. Discontinuous distributions of pathogen species is less likely to occur on these more productive sites than on the drier sites. This pattern is seen in M333d, where only 1 percent of hectares in habitat type group 4 compared to 9 percent of habitat type groups 1, 2 and 3 were rated root disease severity 7, 8, or 9, corresponding to open root disease patches. It was not, however observed in M332a, where all four habitat type groups had less than 3 percent of hectares assigned severity ratings of 7 or higher.

Establishment of new clones of root pathogens is limited more by exclusion of mycelia from substrates already occupied by clones of the same or competitive species than by a paucity of substrates. Only 3 percent of hectares in M332a and 11 percent in M333d were without evidence of root disease visible in aerial photographs. Grand fir, in particular, is nearly always present to provide a suitable substrate for the fungi. Grand fir was among the top three species in at least 67 percent of hectares of M332a and 57 percent of M333d, in the 1975 era sample. Although the pathogens are nearly always in evidence at the stand (or polygon) level, at any one time, most trees will appear outwardly healthy. Large to small groups of dead and dying trees are normally seen within the stand. These represent "hot spots" or clumps of particularly active inoculum. With time, symptomatic trees develop in places that may have gone decades without evidence of infection (van der Kamp 1995, Theis and Nelson 1997).

Fire returns, which are sufficiently frequent to allow western larch to become well-developed as the dominant species in the forest, may serve to reduce fungus biomass somewhat by keeping the size of grand fir and Douglas-fir root systems small, making it difficult for pathogens to maintain biomass. In theory, with prolonged western larch cover, where fairly frequent under burning can keep the grand fir and Douglas-fir trees from reaching large root biomasses, fungus biomass should decline and become discontinuous to the point that a generation of Douglas-fir or Douglas-fir and grand fir dominated, fully-stocked forest could eventually develop on the site.

In this study, a well-stocked, mature Douglas-fir or grand fir stand was based on the well-stocked, sawlog classes used in the 1935-era surveys. As such, they are defined as averaging at least 15 inches DBH with at least 20,000 board feet/acre volume. This is actually a fairly modest stocking level for these habitat types. The SC 3 stand condition with Douglas-fir or Douglas-fir/grand fir forest type was rare overall in our sample areas in both the 1935 era and the 1975 era, constituting less than 3 percent of hectares in both ecosections at both time periods. In habitat type group 4, Douglas-fir or Douglas-fir/grand fir forest types with SC 3 represented 0 percent of hectares in the 1935 era and 7 percent in the 1975 era for M332a; 2 percent in the 1935 era and 6 percent in the 1975 era for M333d.

As in the previous regimes, a generation of Douglas-fir appears to be sufficient to rebuild the fungus biomass sufficiently to again begin selecting against Douglas-fir in subsequent generations. A mixture of generations will develop on a site over the course of a century if the site is not subject to fire. As maturing Douglas-fir are killed by root pathogens and canopy opening develop, seedling Douglas-fir and grand fir will begin growing in the openings. This sequence is seen in 24 percent of Douglas-fir cover type stands that begin in structure class 4 which ended in structure class 2 with Douglas-fir or grand fir cover types (Figure 6.26). Generations become abbreviated in these openings with young trees succumbing before or shortly after reaching cone-bearing age. The forest becomes a mosaic of increasingly uneven-aged patches.

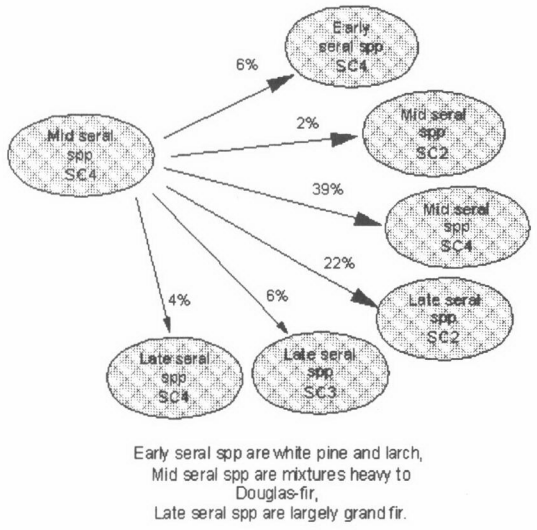
M333d, habitat type group 4: Polygons with moderate to high influence from root pathogens.
Pathways from Douglas-fir/grand fir cover type in large-tree, low density (SC4) structure class.
Percent of hectares, 1935 to 1975.
Early seral spp SC4
6%
Mid seral spp SC4
2%
Mid seral spp SC2
39%
Mid seral spp SC4
22%
Late seral spp SC2
4%
6%
Late seral spp SC4
Late seral spp SC3
Early seral spp are white pine and larch,
Mid seral spp are mixtures heavy to Douglas-fir,
Late seral spp are largely grand fir.

Figure 6.26: Pathways, Douglas-fir/grand fir cover types in structure class 4, habitat type group 4, moderate to high root pathogen influence, M333d.

Since it may take a generation or two before species composition is again shifted mostly away from Douglas-fir and back to western larch or western white pine (with stand replacement fires), large root disease patches may develop as colonies merge. When burning occurs, and sufficient seed source is available for western larch or western white pine to produce significant compositions in the stand initiation phase, the large biomass of root pathogens will again play an important role in removing Douglas-fir, and to some extent, grand fir from the stands..The stage is then set for conversion back to western larch and/or western white pine for, perhaps, two or more centuries.This function was seen on 40 percent of hectares with high to moderate root disease severity in M333d, habitat type 4, which started in SC 1 in the 1935 era and had forest types containing larch or pines in the 1975 era. In the absence of fire, the species composition in the patches is likely to shift fairly quickly toward Douglas-fir and grand fir. This was observed in 90 percent of hectares in M332a and 74 percent of hectares in M333d, habitat type group 4, which had larch or pine forest types in the 1935 era, and increased their relative composition of Douglas-fir and grand fir by the 1975 era. The site occupation by grand fir is eventually likely to be higher than that by Douglas-fir because of significantly longer survival of grand fir in the presence of a large root pathogen biomass.

Moderately cool and moist habitat types, Group 5 (see Appendix A, Figures 18-29). These types also support a virtually continuous distribution of root pathogen colonies. Suitable substrates are in ample supply on most sites. Only 12 percent of sample stands in habitat type group 5 in M333d and none in M332a were rated as having no discernable effects from root disease. Western white pine and Douglas-fir established readily on most of these sites (Haig et al. 1941, Watt 1960) before blister rust had spread into Idaho and Montana. Western white pine was seen to increase it's site dominance as Douglas-fir declined in importance in stands by about age

40 due to selective killing by root pathogens (Haig et al. 1941, Watt 1960). The cause was originally reported as *Armillaria mellea,* but more recent work by Williams and Leaphart (1978), James et al. (1984), Byler et al. (1992) and Lockman (1994) points to combinations of, *Armillaria sp., Phellinus sulphurascens,* and *Heterobasidion annosum.* The *Armillaria* species is most likely *Armillaria ostoyea,* (Morrison et al. 1985, Wargo and Shaw 1985, McDonald et al. 1987) rather than *A. mellea*, a name which was once applied to most parasitic Armillarias in North America. Byler et al. found *Phellinus sulphurascens* (as *P. weirii*) to be more common on western redcedar, western hemlock, and grand fir climax habitat types (groups 4 and 5, in this classification system) than on other habitat types. Like *Armillaria*, *P. sulphurascens* is probably mostly dispersed across sites rather than occuring in discrete patches (Thies and Nelson 1997).

Of the hectares that had Douglas-fir in the forest type in the 1935 era, 45 percent in M332a and 53 percent in M333d had no Douglas-fir in the forest type. Root disease influence in these transitions was rated moderate to high on 97 percent of the sample hectares in M332a and 99 percent of the M333d sample. Although grand fir is more likely than Douglas-fir to reach maturity, it usually manages to produce only moderately-stocked stands dominated by grand fir at maturity. This can be seen in the low proportion (25 percent) of the hectares in SC 1 or SC 2 in the 1935 era with grand fir as the primary component, which had progressed to SC 3 by the 1975 era, still were primarily grand fir forest types (Figure 6.27). Most of those which progressed to SC 3 had large components of western redcedar or western hemlock, although some amount of grand fir was usually present as well. So, although the grand fir generally maintained it's presence in the stand over the 40-year study period, it declined in relative stocking. Heavy fungus biomass is probably the main reason grand fir is also killed at a rapid rate on these sites.

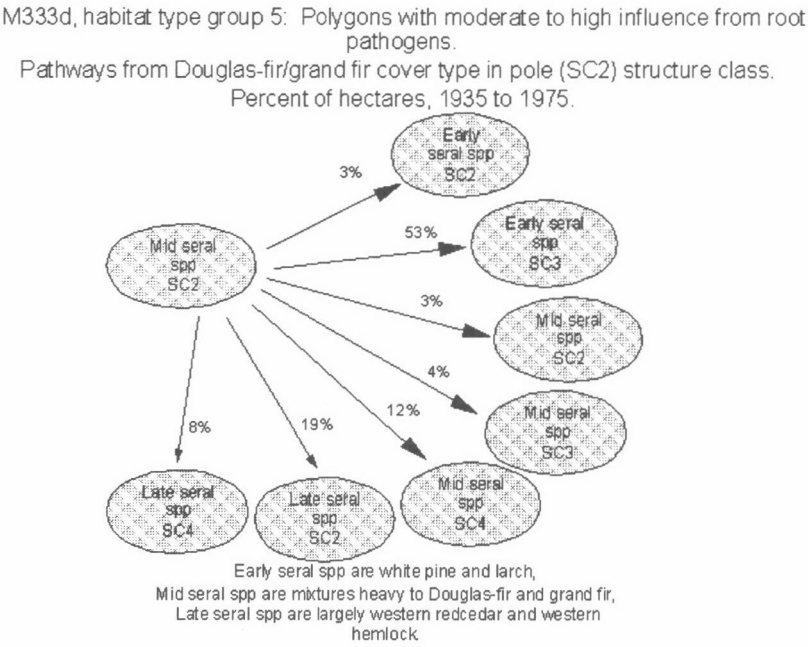
M333d, habitat type group 5: Polygons with moderate to high influence from root pathogens.
Pathways from Douglas-fir/grand fir cover type in pole (SC2) structure class.
Percent of hectares, 1935 to 1975.
Early seral spp SC2
3%
Mid seral spp SC2
53%
Early seral spp SC3
3%
Mid seral spp SC2
4%
Mid seral spp SC3
8%
19%
12%
Late seral spp SC4
Late seral spp SC2
Mid seral spp SC4
Early seral spp are white pine and larch,
Mid seral spp are mixtures heavy to Douglas-fir and grand fir,
Late seral spp are largely western redcedar and western hemlock

Figure 6.27: Pathways, Douglas-fir/grand fir cover types in structure class 2, habitat type group 5, moderate to high root pathogen influence, M333d.

The situations represented by the 25 percent of hectares in which grand fir maintained it's site dominance while progressing to SC 3 are probably mostly because of lower initial root

pathogen biomass. All such stands in this study had been assigned western white pine, lodgepole pine or western larch cover types in the 1935-era survey. Sites that have had prolonged cover dominated by western white pine and western larch, in particular once were a common occurrence on these habitat types (Haig et al. 1941). Root pathogen biomass probably decreased significantly under extended periods with these cover types. As succession eventually lead toward shade-tolerant species, the low pathogen biomass would be expected to allow occasional development of a grand fir stand that nearly fully occupied a site at maturity. Site occupations by pines and larch were probably highly significant part of this successional regime, providing periodic breaks in the expansion of root pathogen colonies and even leading to occassional death of a clone. The appearance of white pine blister rust in white pine forests, combined with the near-elimination of fires (which once favored the regeneration and survival of larch and pines), have provided exceptional conditions for the expansion and intensification of root pathogens.

Even on sites with initially low fungus biomass, a century of site-occupation by grand fir eventually leads to sufficient increases in root pathogens to cause the decline of grand fir and replacement with increasingly greater proportions of western redcedar and/or western hemlock forest, which regenerate freely in the shade of the deteriorating grand fir overstory. Evidence of this is seen in transitions from the Douglas-fir/grand fir forests in structure class 3 to early-, mid- or late-seral species, none remaining in structure class 3 (Figure 6.28). This process may take more than one generation of grand fir-dominated stands to complete. In contrast to Douglas-fir components, grand fir has tended to remain a component throughout the 40-year study period. Of the 1,935 hectares in the M333d sample in the 1935 era, 92 percent still had grand fir as part of the forest type in the 1975 era. Similarly, 68 percent of the grand fir forest types remained at least partly grand fir types in M332a. Western redcedar or western hemlock were the predominant forest types on the few hectares that did loose the grand fir component in M333d (93 percent). In M332a, 90 percent of the forest types containing grand fir in the 1935-era survey that lost the grand fir component by the 1975 era, had converted to western redcedar forest type. High to moderate root disease influence on these transitions were seen on 100 percent of sample hectares in M333d and 89 percent of hectares in M332a. Heavy fungus biomass would likely have developed under these conditions.

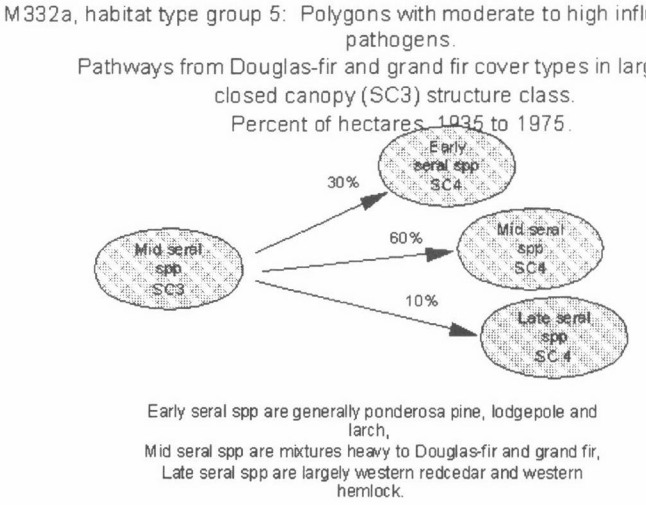
M332a, habitat type group 5: Polygons with moderate to high influence from root pathogens.
Pathways from Douglas-fir and grand fir cover types in large-tree, closed canopy (SC3) structure class.
Percent of hectares, 1935 to 1975.
Mid seral spp SC3
30%
Early seral spp SC4
60%
Mid seral spp SC4
10%
Late seral spp SC4
Early seral spp are generally ponderosa pine, lodgepole and larch,
Mid seral spp are mixtures heavy to Douglas-fir and grand fir,
Late seral spp are largely western redcedar and western hemlock.

Figure 6.28: Pathways, Douglas-fir/grand fir cover types in structure class 3, habitat type group 5, moderate to high root pathogen influence, M332a.

Western redcedar is fairly resistant to killing by root pathogens once past the sapling stage. Mature stands of cedar are likely to be self-maintaining with fire as the primary process for change once cedar has achieved site dominance. The situation may be quite different for western hemlock, however. While western hemlock is more resistant to killing by the common root pathogens in this area, we have seen enough examples of even the first mature generation of western hemlock on sites with high biomass of *A. ostoyae* and *H. annosum* to know that they are unlikely to be able to maintain an indefinite occupation of a site. Our sample of M332a had no western hemlock forest type but there were 4,316 hectares with western hemlock forest type in our sample of M333d in the 1975 era. In western hemlock forest type (those with at least 80 percent western hemlock basal area), although the rate of root disease severity rated as 0 was relatively high at 42 percent of hectares, there were stands with heavy root disease as well (Table 6.30). Root disease patch development in mature hemlock forests is similar to that observed in grand fir forests. Due to the prevalence of western white pine on these habitat types, however, large disease patches were probably relatively infrequent as compared to grand fir habitat types, historically. The ability of western hemlock forests to maintain canopy closure for extended periods is unknown at this time, but results from this study indicate that there is potential for the eventual decline of western hemlock as well. Western hemlock was not specified as a forest type in the 1935-era survey methods, but cover type 4 was designated as western hemlock/grand fir. Only 239 hectares of our sample were classified as cover type 4 in the 1935 era. These same stands had root disease severities ranging from 0 to 8 in the 1975-era survey; the weighted average severity was 5. Based on their polygon classes in the 1935 era their root disease severities could be expected to have averaged about 3. This is higher than the overall rate of increase for M333d based on probable 1935-era disease levels. Continued monitoring of established permanent plot in this ecosection may eventually support or refute the apparent trends we have observed in this limited sample. Since western hemlock is increasingly an important forest type in ecosection M333d, it will be imperative to better understand it's ability to withstand heavy root pathogen inoculum loads.

Table 6.30: Root disease severity in stands with western hemlock forest type (greater than 80 percent western hemlock basal area).

Root Disease Severity	Proportion of Hectares
0	.42
1	.16
2	<.01
3	.17
4	.13
5	.09
6	.03
7	>.01

Persistent root disease patches

A proportion of this habitat type group will develop into root disease patches that remain relatively stable, probably for several generations of trees. Generations, in this case, are fairly short because trees die a young ages and the patches are continuously regenerated by seedfall from surrounding stands. In M332a, a significant number of polygons with western redcedar habitat types, Douglas-fir forest type and seedling/sapling structure class (SC 1) were apparently stable root disease patches. This is evident in 62 percent of the hectares of this polygon class that were still in the seedling/sapling stage 40 years later. These patches still had Douglas-fir or grand fir as forest type components with most remaining in early to mid-seral compositions. Similar transitions were observed in M333d with 60 percent of hectares in the polygon class remaining in forest types containing significant Douglas-fir or grand fir and structure class 2 (Figure 6.29). Root disease severity on those sites averaged 7.6 in the 1975 era. This is an indication that the root pathogens have functioned on these sites to "stall" or suspend succession. The root pathogens on these sites will chronically kill trees, effectively preventing most of the trees from growing into pole size classes. The result is that the stands reach neither the pole nor mature structure classes. Regeneration in openings created by mortality is dominated by Douglas-fir or grand fir as evidenced by the sites remaining in Douglas-fir and grand fir forest types and seedling/sapling structure class after 40 years. This cycle is potentially continuous, probably requiring events such as stand-replacing fire to establish pines or larch, thereby disrupting the supply of hosts. With the low availability of host, root pathogen biomass would eventually decline.

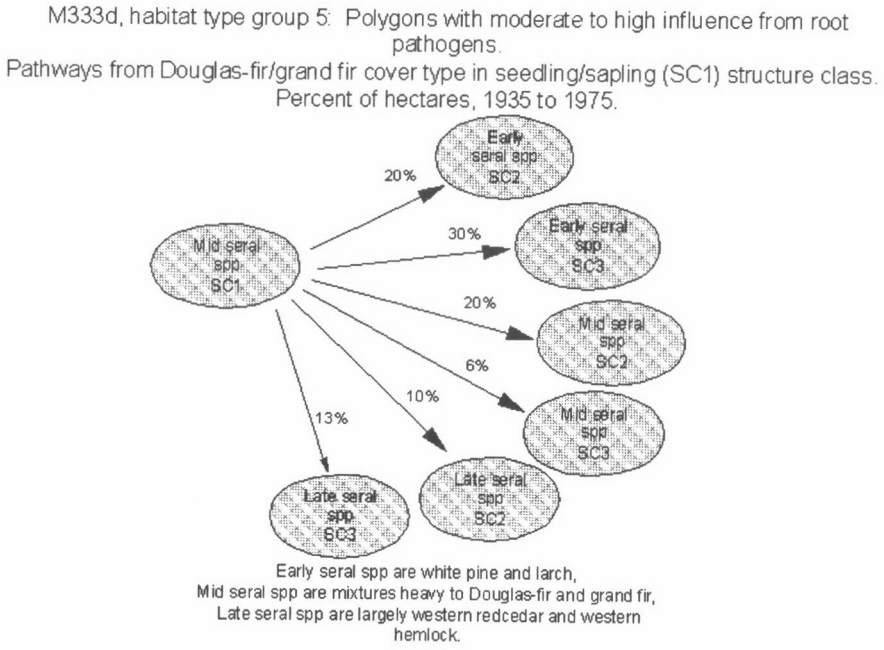
M333d, habitat type group 5: Polygons with moderate to high influence from root pathogens.
Pathways from Douglas-fir/grand fir cover type in seedling/sapling (SC1) structure class.
Percent of hectares, 1935 to 1975.
Early seral spp SC2
Early seral spp SC3
Mid seral spp SC1
Mid seral spp SC2
Mid seral spp SC3
Late seral spp SC2
Late seral spp SC3
20%
30%
20%
6%
10%
13%
Early seral spp are white pine and larch,
Mid seral spp are mixtures heavy to Douglas-fir and grand fir,
Late seral spp are largely western redcedar and western hemlock.

Figure 6.29: Pathways, Douglas-fir/grand fir cover types in structure class 1, habitat type group 5, moderate to high root pathogen influence, M333d.

Root disease and Douglas-fir beetle

Interaction of root diseases and Douglas-fir beetle is evident in polygons the class, Douglas-fir habitat type (HT 2 or 3)/Douglas-fir cover type (CT DF)/structure class mature, low density (SC 4) in the 1935 era. In M333d, the root disease severity average expected for the polygons which were assigned to this class in the 1935 era is 4.7 and the disease severity assigned to the same sites in the 1975 era averaged 4.9. According to the Douglas-fir beetle API for this class, 17 percent of the stands were dense enough to support a Douglas-fir beetle outbreak and all of the stands in the class were prone to Douglas-fir beetle single or small-group killing action. One-half of the hectares converted to Douglas-fir to ponderosa pine cover type over the 40-year period.

In M332a, root disease severities in this starting polygon class were lower than M333d in the 1935 era, calculated to have been about 2.6. The increase in root disease severity may have been greater, with these polygons rated an average of 3.6 in the 1975 era. The probability of a Douglas-fir beetle outbreak was probably much higher in the Douglas-fir habitat type/Douglas-fir CT/SC 4 in M332a than in M333d. A high probability for Douglas-fir beetle outbreak was assigned to 78 percent of hectares in this polygon class based on 1935-era conditions. The combination of relatively lower root disease influence and higher Douglas-fir beetle influence in M332a than in M333d still resulted in 40 percent of hectares in this starting polygon class converting from Douglas-fir to ponderosa pine cover type.

Without the influence of root diseases and Douglas-fir beetle, these sites would have been expected to remain Douglas-fir cover types and in the absence of ground fire, they would be expected to increase in Douglas-fir density. Ponderosa pine is a shade-intolerant seral species in this habitat type group. Root diseases and Douglas-fir beetle are both expected to function to

maintain seral species such as ponderosa pine, where they are present in the stands. diseases will selectively kill Douglas-fir of any age from such a species mix, and Douglas-fir beetle will selectively kill mature Douglas-fir. Together, they can be expected to enhance the survival of the pines by reducing the lateral competition. This function appears to have been strongly expressed in this polygon class in both M332a and M333d.

About 40 percent of the hectares in the Douglas-fir habitat type/Douglas-fir CT/SC 4 polygon class in each ecosection, remained in the same class after 40 years. The density did not increase, as may have been expected in the absence of ground fire. The 1975-era root disease severity average of 4.9 in M333d and 3.6 in M332a indicate that root disease-caused mortality of Douglas-fir probably resulted in continuous low stocking of less than 20,000 boardfeet/acre. This would generally be considered a poor mature-stand stocking for this site quality.

Trends in root disease severity in the 1935-era survey subsample

Overall trends in root disease severity for polygons in habitat type group 5 that were surveyed in both 1935 and 1975 eras indicate a small increase from 1935 to 1975 eras and from 1975 to 2015. The average severity for the subsample of M332a that was surveyed in both 1935 and 1975 eras indicates an increase from the calculated average of 4.3 in the 1935 era to the measured average of 4.8 in the 1975 era. When this subsample is projected forward another 40 years, a smaller increase to an average of 5.0 is expected. In M333d, the calculated average of 2.9 in the 1935 era, increased to 3.8 in the 1975 era and, when projected for another 40 years, may decline slightly to 3.7. The apparent deline in severity in M333d is in response to a predicted increase in western redcedar and western hemlock cover types. Many of these polygons had Douglas-fir and grand fir cover types in the 1975 era and these were largely western white pine cover types in the 1935 era.

Most of the hectares of this habitat type group that were in polygon classes in the 1935 era associated with low levels of disease severity had progressed to moderate levels of severity by the 1975 era. Relatively few polygons progressed to disease severity classes indicative of more than 90 percent loss of forest canopy (high disease severity). The species mixtures possible on these sites probably have an ameolorating effect as other species fill in behind dying Douglas-fir and grand fir preventing the formation of large areas of very low canopy closure. When these polygons are projected forward, this trend appears likely to continue through 2015 (Table 6.31) with the vast majority of polygons falling in severity classes 3 to 6 (corresponding to 10 percent to 75 percent loss of canopy cover).

Table 6.31: Distribution of root disease severity averages for polygon classes represented in the 1935 era (calculated based on actual polygon class), 1975 era (measured), and 2015 (calculated based on projected outcome). Proportions of hectares in the subsample.

	M332a (1,202.6-hectare subsample)			M333d (10,024.8-hectare subsample)		
RRSV	1935	1975	2015	1935	1975	2015
0	.00	.00	.00	.00	.02	.01
1	.01	.02	.00	.03	.08	.01

2	.15	.03	.01	.49	.31	.14
3	.08	.01	.01	.33	.25	.29
4	.10	.30	.35	.14	.20	.36
5	.61	.47	.52	.00	.10	.11
6	.11	.12	.04	.00	.04	.09
7	.01	.01	.03	.00	.01	>.01
8	.00	.04	.04	.00	>.01	>.01
9	.00	.00	.00	.00	>.01	>.01

Cold and moist habitat types: Group 7 (see Appendix A, Figures 30-42). Root pathogens are a nearly constant presence in these cool, moist habitat types. Only 2 percent of the 1,012 hectares in M332a and 4 percent of 3,559 hectares in M333d samples in the 1975 era were rated as having no visible root disease effects. The average root disease severity (RRSV) in this group was 4.5 in M332a and 3.2 in M333d. The lowest root disease severities tend to occur in early-seral forest types and the highest severities are mostly found in late-seral forest types. An exception is the mid-seral types containing Douglas-fir but no earlier seral species. In these types, severities range from moderate (RRSV 3) to very high (RRSV 6 and 7). These data indicate that root pathogens are well-distributed across sites of this habitat type group.

The constancy, and often high severity of root diseases indicate an important role for root pathogens in forest succession in habitat type group 7. Between the 1935 era and the 1975 era, 64 percent of the sample hectares for M332a and 38 percent of M333d underwent changes that were probably largely driven by root pathogens. Where root pathogens were an important influence, stalling structure development in relatively young structures or moving backward from large tree structures to smaller and younger structures were prevalent roles (Figures 6.30 and 6.31). These pathways occurred on 37 percent of the root disease influenced hectares in M332a and 45 percent in M333d. The outcome of these functions is evident in the relative proportion of M333d that was in strucure class 1 in the 1975 era (Table 6.32).

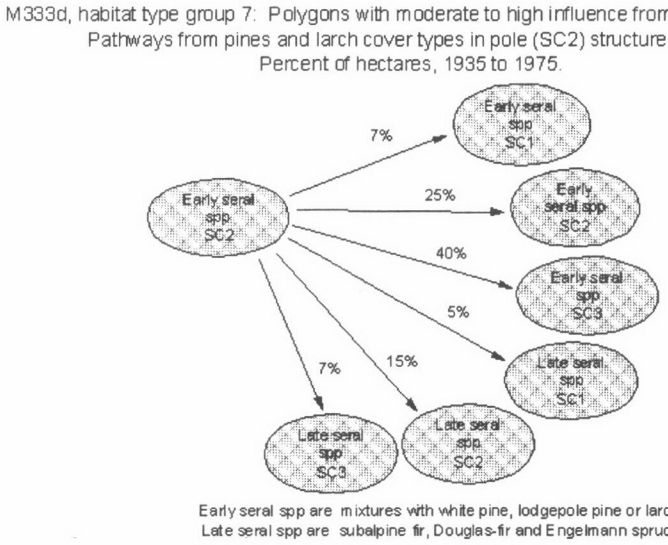
M333d, habitat type group 7: Polygons with moderate to high influence from root pathogens.
Pathways from pines and larch cover types in pole (SC2) structure class.
Percent of hectares, 1935 to 1975.
Early seral spp SC2
7%
Early seral spp SC1
25%
Early seral spp SC2
40%
Early seral spp SC3
5%
Late seral spp SC1
7%
15%
Late seral spp SC3
Late seral spp SC2
Early seral spp are mixtures with white pine, lodgepole pine or larch,
Late seral spp are subalpine fir, Douglas-fir and Engelmann spruce.

Figure 6.30: Pathways, pine and larch cover types in structure class 2, habitat type group 7, moderate to high root pathogen influence, M333d.

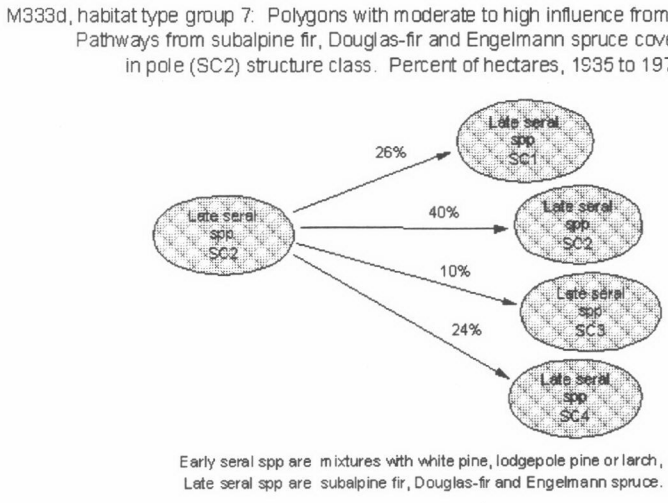
M333d, habitat type group 7: Polygons with moderate to high influence from root pathogens.
Pathways from subalpine fir, Douglas-fir and Engelmann spruce cover types
in pole (SC2) structure class. Percent of hectares, 1935 to 1975.
Late seral spp SC2
26%
Late seral spp SC1
40%
Late seral spp SC2
10%
Late seral spp SC3
24%
Late seral spp SC4
Early seral spp are mixtures with white pine, lodgepole pine or larch,
Late seral spp are subalpine fir, Douglas-fir and Engelmann spruce.

Figure 6.31: Pathways, subalpine fir, Douglas-fir, and Englemann spruce cover types in structure class 2, habitat type group 7, moderate to high root pathogen influence, M333d.

Most of the hectares in structure class 0 were coded as recent or older burns (15 or 16) in the 1935-era survey. The proportions of these hectares which underwent changes consistent with moderate to high root disease severity were consistent with the proportion of the rest of this habitat type group that is rated moderate to high in root disease severity. Root disease severities 4 -7 (representing moderate to high classes) were assigned to 42.9 percent of M332a habitat type group 7, corresponding to 42.7 percent of hectares of SC 0 with moderate to high influence, likewise, 21.3 percent of M333d corresponded to 16.7 percent with moderate to high influence.

This is an important relationship to understand because the root disease severity cannot be directly assigned to structure class 0. Even though the biomass of root pathogens may have remained high in the root systems of killed trees following the fire, there are too few live trees from which to observe effects root disease in the aerial photographs. It would appear that, at least within this habitat type group, the root disease severity rates for the forested portions are indicative of the future influence of root disease in the burned portions as well.

All of the polygons of M332a starting in structure class 0 that did not have significant influence from root disease, were in structure class 2 by the 1975 era. Those in SC 0 with moderate to high influence from root disease nearly all progressed only to SC 1 (63 percent) and the remainder were in SC 4. Less striking contrast was seen in M33d: here, 50 percent of hectares without root disease influence progressed from SC 0 to SC 2, and 95 percent of those with root disease influence, did so. However, the remaining 5 percent of root disease-influenced hectares were found in SC 1 in the 1975 era, while 23 percent of those not influenced by root disease had progressed to SC 3 and 27 percent were in SC 4. So, while moderate to severe root disease causes a significant structure stalling effect in both M332a and M333d, the afflicted stands in M332a tended to stall in SC 1 while those in M333d were more likely to reach SC 2. The influences of root disease in M333d were somewhat confounded by those of white pine blister rust. Where western white pine was an important stand component the death of white pines in any size class tends to produce similar structure changes to those resulting from root disease. Significant blister rust influence was seen on 23 percent and 37 percent of root disease hectares that had significant root disease succession influences in M332a and M333d, respectively.

Table 6.32: Changes in proportions of structure classes from the 1935 era to the 1975 era, without root disease influences and with moderate to high root disease influence.

M332a	Without Root Disease Influence		With Moderate to High Influence	
Structure Class Code	1935-era Proportion	1975-era Proportion	1935-era Proportion	1975-era Proportion
0	.16	.00	.15	.00
1	.20	.00	.00	.11
2	.30	.36	.44	.41
3	.16	.41	.12	.32
4	.18	.23	.29	.16

M333d	Without Root Disease Influence		With High to Moderate Influence	
Structure Class Code	1935-era Proportion	1975-era Proportion	1935-era Proportion	1975-era Proportion
0	.40	.00	.11	.01

1	.15	.00	.13	.16
2	.20	.36	.15	.50
3	.02	.42	.03	.13
4	.24	.22	.58	.20

Root disease severity trends in habitat type group 7. The trends in root disease severity from the 1935 era to the 1975 era in those polygons that were sampled in both time periods is particularly interesting. For M332a, the average of root disease severities calculated for the polygons based on 1935-era polygon classes indicate a substantial increase from the 1935 era to the 1975 era and then leveling off for the subsequent 40 years through 2015 (Table 6.33). The calculated severity based on polygon classes in the 1935 era was 3.5; the measured severity average for the same polygons in the 1975 era was 4.5; and the projected average severity for 2015 was also 4.5. For M333d., a similar increase was calculated from the 1935-era to 1975-era data with a continued trend toward higher disease severities through 2015. The calculated average severity rating for the 1935 era was 2.4; the actual 1975-era severity average was 3.6; and a projected average severity in 2015 was 3.9.

Table 6.33: habitat type group 7; distribution of root disease severity classes calculated for the 1935 era, measured in the 1975 era, and projected for 2015.

HT Group 7	M332a Proportion of 1006.7-hectare Subsample			M333d Proportion of 3383.3-hectare Subsample		
Root Disease Severity Rating	1935 era	1975 era	2015, Projected	1935 era	1975 era	2015, Projected
0	.00	.07	.00	.12	.00	.00
1	.20	.08	.14	.26	.06	.02
2	.11	.16	.08	.14	.15	.11
3	.15	.11	.08	.29	.27	.23
4	.15	.13	.10	.16	.23	.32
5	.35	.24	.47	.00	.18	.19
6	.05	.21	.12	.04	.04	.05
7	.00	.01	.01	.00	.05	.08
8	.00	.00	.00	.00	.01	>.01

Cool and moderately dry habitat types: Group 9. Root pathogens are prevalent in this habitat type group, although less so than in habitat type group 7. The sites are colder and moisture limited, which probably limits the ability of the fungi to expand their colonies. Lower stocking may also be limiting to the pathogens by making tree-to-tree movement more difficult.

The effect of large components of lodgepole pine is similar to that of ponderosa pine on the warmer but also moderately dry habitat types, limiting root pathogen biomass accumulation. At the low end of fire return intervals of about 50 years (Fisher 1987), a fairly continuous cover of lodgepole pine with a smaller component of western larch and Douglas-fir would lead to declines in root pathogen biomass and fragmented clones. But at the upper end of fire intervals, 130-years, the proliferation of subalpine fir and large root mass size achieved by some of the Douglas-fir probably ensured occasional enlargement of clones and aggressive attacks on young subalpine fir with relatively more gradual death of large Douglas-fir. These buildups in pathogen biomass subsequently ensure better sruvival of pines and larch by limiting the potential of subalpine fir and Douglas-fir to compete. This in turn ensures a more substantial shift toward early seral species with the next fire. The loss of fire during the years 1935-1975 may not be substantially different from the natural events on these sites, based on the work of Fisher (1987), and the high rate of recent burning, especially in M333d, at the start of our study interval (1935-1975). If this is true, then the substantial buildup of fungus biomass that has accompanied the increases in subalpine fir and, perhaps, Douglas-fir may represent the expected increase between fires.

Sample polygon statistics (see Appendix A, Figures 43-50). Much of the sample area for M333d (41 percent) of this habitat type group had been recently burned in the 1935 era (Table 6.34). Of these hectares, the majority (41 percent) was classified as lodgepole pine in the 1975 era, with significant proportions also classified as subalpine fir (31 percent) or grand fir (9 percent). Western white pine cover type made up 13 percent of the sample in the 1935 era. About half (47 percent) of these hectares had subalpine fir cover type in the 1975 era, with 23 percent becoming lodgepole pine and 17 percent remaining white pine. Of the 14 percent that was lodgepole pine in the 1935 era, nearly a majority remained lodgepole pine forty years later. The rest of the hectares which had been lodgepole pine cover type were about evenly split among Douglas-fir, subalpine fir and western larch. Subalpine fir cover type had been assigned to 16 percent of hectares, and these mostly (74 percent) remained subalpine fir, with a few changing to lodgepole pine (17 percent). Larch/Douglas-fir made up 8 percent of the 1935 era sample and about half of these had converted to subalpine fir cover type by the 1975 era; another third had converted to lodgepole pine and 18 percent became Douglas-fir cover type. None remained larch/Douglas-fir. The net result of these changes was that 76 percent of hectares became either subalpine fir cover type or lodegpole pine cover types by the 1975 era, with Douglas-fir, grand fir, and western white pine about equal as minor cover types. When projected forward to 2015 based on polygon class, the subalpine fir cover types mostly remain subalpine fir. About a fourth of the subalpine fir cover type converted to lodgepole pine or western white pine cover types. This function was largely through the action of root pathogens killing subalpine fir, thereby increasing the importance of the pines in the species composition. In these transitions the majority of hectares both start and end in structure class 2 (Figure 6.32).

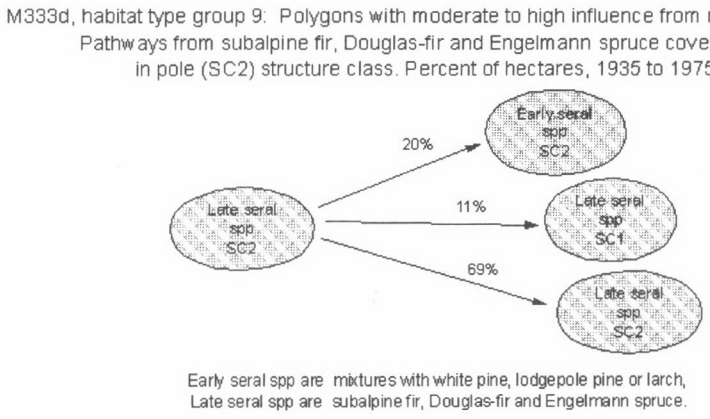
M333d, habitat type group 9: Polygons with moderate to high influence from root pathogens.
Pathways from subalpine fir, Douglas-fir and Engelmann spruce cover types
in pole (SC2) structure class. Percent of hectares, 1935 to 1975.
Late seral spp SC2
20%
Early seral spp SC2
11%
Late seral spp SC1
69%
Late seral spp SC2
Early seral spp are mixtures with white pine, lodgepole pine or larch,
Late seral spp are subalpine fir, Douglas-fir and Engelmann spruce.

Figure 6.32: Pathways, subalpine fir, Douglas-fir, and Englemann spruce cover types in structure class 2, habitat type group 9, moderate to high root pathogen influence, M333d.

With the movement away from the nonforest structure class in M333d, the average root disease severity probably jumped fairly sharply between the 1935 era and the 1975 era. The calculated average severity in the 1935 era was 2.3, and in the 1975 era the measured average was 3.5. This increase would be mostly a function of stands growing into a structure in which the disease effects are more visible rather than real increases in root pathogen biomass. The fungi undoubtedly remained viable in root masses left after the pre-1935 burns, and continued to be active in the succeeding generation. According to projected classes in 2015, it appears the root disease severity may level off at about 3.5. With few hectares starting in nonforest structure classes, most polygons had low to moderate levels of disease severity and only a few stands (roughly 5 percent of hectares) are expected to progress to relatively severe levels of root disease (RRSV 7 - 9). The polygons which are expected to progress to the most severe levels of root disease started with lodgepole pine, Douglas-fir, or larch/Douglas-fir cover types, and are projected to progress by 2015 to Douglas-fir cover type or to seedling or sapling structutres with subalpine fir or grand fir cover types.

Table 6.34: Changes in cover type in habitat type group 9; 1935 era to 1975 era and projected for 1975 to 2015. Trends based on same areas surveyed in both the 1935 era and the 1975 era.

	M332a (1,746.1-hectare subsample)			M333d (2873.9-hectare subsample)		
Cover type	**1935 era**	**1975 era**	**2015-era**	**1935 era**	**1975 era**	**2015-era**
Non-forest, recent burn	.08	0	0	.41	.04	.01
Subalpine fir	.17	.36	.58	.16	.41	.46
Lodgepole pine	.45	.40	.26	.14	.35	.29
Western white pine	.05	0	0	.13	.04	.05

Larch/Douglas-fir	.01	0%	.01	.08	<.01	.07
Douglas-fir	.16	.17	.16	.04	.06	.10
Grand fir	0	.01	0	<.01	.06	.01
Ponderosa pine	.07	.03	0	0	0	0
Mountain hemlock mix	0	0	0	.02	<.01	<.01
Engelmann spruce	.02	.02	.01	.01	.03	1%

The average root disease severity in this habitat type group in the 1975 era sample of M332a was 2.9, with virtually all stands showing some signs of root disease. In our sample of M332a, relatively little of the area had been involved in recent burns in the 1935 era, with a total of only 8 percent found in a non-forested condition. Nearly half of hectares were classified as lodgepole pine cover types: however, and about a third of those were in seedling/sapling structure classes (SC 1). Most (60 percent) of the hectares of lodgepole pine cover type in the 1935 era were still lodgepole pine cover type in the 1975 era. Most of the remainder had converted to subalpine fir (36 percent). Both subalpine fir and Douglas-fir cover types were moderately important in this sample in the 1935 era, consitituting 17 percent and 16 percent of hectares, respectively (Table 6.34). Both cover types also increased somewhat by the 1975 era, to 22 percent and 21 percent, respectively, These types were derived from white pine, and lodgepole pine cover types, primarily. With these increases in subalpine fir and Douglas-fir, it is surprising that the average root disease severity appears to have increased very little, if any, from 2.7 in the 1935 era to 2.9 in the 1975 era. A continued slow movement toward more subalpine fir and stable proportion of Douglas-fir cover type is projected for the period from 1975 to 2015. Despite the increase in subalpine fir, the root disease severity is expected to remain about the same throughout the period.

Trends in Root Disease Succession Functions

Considerably less change in cover type is expected in the approximately 40 year period from 1975 to 2015. A 6,315-hectare subsample of M332a and 22,003-hectare subsample of M333d were surveyed in both the 1935 era and the 1975 era. For polygons with evidence of root disease activity, trends in cover types and structure classes are indicative of the ways in which root pathogens function. For example, one common cover type change was described as "increasing climax components of stands." This is seen in cover type changes from early seral tree species toward mid- or late-seral species, or from mid-seral species to late-seral species. In the function described as "maintain early seral components" there may be a change in cover type or there may not, but the cover types at the beginning and end of the period include early seral species (e.g., white pine, ponderosa pine, lodgepole pine, and western larch). A third type of function, "increase in early-seral composition," is indicated in a transition from a Douglas-fir/ponderosa pine cover type to at least 80 percent ponderosa pine cover, or from a Douglas-fir cover type to a Douglas-fir/ponderosa pine cover type.

While only about a third (38 percent) of hectares in the sample of M332a maintained the same cover type from the 1935 era to the 1975 era, over half (58 percent) of hectares are predicted to retain the same cover type from 1975 to 2015 (Table 6.35). Similarly, in M333d, only 10 percent of hetares remained in the same cover type class from the 1935 era to the 1975 era where root pathogens were visibly active. But the projected changes from 1975 to 2015 indicate that about 40 percent of hectares will remain the same cover type despite active root disease.

Far fewer hectares are expected to move more toward climax composition in the second 40 years than did in the first 40 years (Table 6.35). Much of this change in trends is probably due to the large proportion of hectares which had already moved substantially toward climax composition in the first 40 years so they contribute to the large increase in stable cover types during the second 40 years. An interesting and potentially important trend in root disease-affected stands are the functions which maintain or increase proportions of early-seral species.

There is a large drop in the "maintain early-seral components" function in M333d indicated (Table 6.35) from the first 40 years to the second 40 years, which can be seen in the decline in the abundance of western white pine. In the first 40 years, the white pine cover type remaining white pine cover type accounted for nearly 2,500 hectares of this function, but this transition type dropped to about 1,500 hectares during the second 40 years. The cumulative effect of white pine blister rust undoubtedly accounts for most of this trend.

The only other single pathway that was important in both 40 year periods was lodgepole pine remaining lodgepole pine. In both M332a and M333d, this pathway remained fairly steady at 49 percent of the lodgepole pine type in the first 40 years and 61 percent in the second 40 years (Table 6.35).

Table 6.35: Measured and projected trends in cover type occurring in polygons with obvious root disease activity. Measured trends were from the 1935 era to 1975 eras (first 40 years), and projected trends were from 1975 to 2015 (second 40 years).

	M332a (proportion of 6,314.8-hectare subsample)		M333d (proportion of 22,002.9-hectare subsample)	
Cover Change Function	**First 40 yrs**	**Second 40 yrs**	**First 40 yrs**	**Second 40 yrs**
Increase climax components	.52	.23	.55	.26
No change in cover	.21	.47	.10	.39
Maintain early-seral components	.20	.19	.30	.18
Increase relative proportion of early-seral components	.07	.11	.05	.16

In M333d, of those stands that underwent an increase in climax components, about a third also remained the same in structure or underwent normal changes in structure toward larger trees and closed canopies. Another third of these stands (as proportion of hectares) either stalled in early structure classes or moved toward structures typified by younger and smaller trees. About a quarter of hectares that increase in climax components ended in structure class 4, indicative of canopy closure having been prevented as stands moved into mature tree structures. Both of these

latter two functions are typically associated with moderate to severe root disease. Although the proportion of stands that are predicted to increase in climax composition from 1975 to 2015 is considerably less than that for 1935-1975 eras, the structure changes on these hectares is expected to remain proportionally similar between the two time periods (Table 6.36).

Table 6.36: Major categories of succession functions in polygons with initial root disease severity ratings greater than 0. Actual changes from 1935 to 1975 eras (first 40 years) and projected changes from 1975 to 2015 (second 40 years) in proportions of hectares.

		M332a (6,314.8 hectares)		M333d (22,002.9 hectares)	
Cover Change	**Structure Change**	**First 40 yrs**	**Second 40-yrs**	**First 40 yrs**	**Second 40-yrs**
Increase climax	Same/normal	.45	.52	.29	.29
	Stall/toward small	.35	.24	.38	.39
	Prevent closure	.20	.20	.18	.15
Cover stable	Same/normal	.69	.61	.12	.30
	Stall/toward small	.13	.13	.51	.36
	Prevent closure	.18	.27	.18	.22
Maintain seral	Same/normal	.56	.54	.22	.34
	Stall/toward small	.30	.19	.64	.47
	Prevent closure	.14	.26	.13	.11
Increase seral	Same/normal	.56	.40	.39	.34
	Stall/toward small	.31	.22	.37	.48
	Prevent closure	.13	.38	.24	.17

In M332a, polygons that did not undergo a change in cover type also tended to remain in the same structure class or progress toward mature, closed-canopy conditions (Table 6.37). This accounted for 69 percent of the hectares that did not change cover type in the interval between 1935 and 1975 eras, and an expected 61 percent in the subsequent 40 years. This was a relatively minor function in M333d; however, where the largest share of hectares that did not have a cover change were stalled in young or small-tree structures (SC 1 or 2) or had moved backward from a large-tree structure (SC 3 or 4) to a young or small-tree structure. This is the type of stand composition and structure expected in polygons with high levels of root pathogen activity. The majority of hectares that had no cover change but moved backward from large- to small-tree structures had started in subalpine fir, grand fir, or Douglas-fir cover types with beginning structure

class 4, indicating they were probably in fairly advanced stages of root disease development at the beginning of the interval. The average root disease severity of these polygons at the start was 4.3, a fairly high average. This trend continues in the projections, but with a larger proportion of hectares stalled in young, small-tree classes.

Where the combination of maintaining or increasing seral species with stalling or moving backward to smaller trees occurs, the majority of hectares essentially become root disease patches with scattered large seral-species trees that are left to dominate the canopy as the root disease-susceptible Douglas-fir and true firs die. The understory is dominated by young Douglas-fir and true firs in the 1975-era stands. On habitat types in which these species are not climax, the understory is expected to eventually shift increasingly toward cedar, and western and mountain hemlock. Few of the hectares had progressed to this stage by the 1975-era survey.

Table 6.37: Influence of root diseases on structure in polygons with initial root disease severity ratings greater than 0. Actual changes from the 1935 to 1975 eras (first 40 years) and projected changes from 1975 to 2015 (second 40 years): proportions of hectares.

	M332a (proportion of 6314.6-hectare subsample)		M333d (proportion of 22002.9-hectare subsample)	
Structure Change Function	**First 40 yrs**	**Second 40 yrs**	**First 40 yrs**	**Second 40 yrs**
Structure stable (no change)	.31	.39	.05	.16
Normal change to larger trees with nearly closed canopies	.18	.12	.20	.15
Stand closure prevented (low canopy density results)	.16	.18	.17	.17
Largest trees die; move toward young, small-tree classes	.13	.09	.16	.17
Structure stalled in young, small-tree class	.12	.09	.28	.23
Large-tree structure; increase in canopy density	.08	.05	.13	.07
Large-tree structure; decrease in canopy density	.01	.08	.01	.05

In both ecosections, structure trends in root disease-affected stands are expected to be similar in the second 40 years to those observed in the first 40 years (Table 6.37). The greatest change in trends is an increase in stable structures that results in polygons with the large-tree, closed canopy structure (SC 3) remaining so. These polygons have a moderately high root disease severity average of 3.8 at the beginning of the period, and are projected to end with about the same level of severity, 3.6, at the end of the period. This is in contrast to the polygons which are expected to stall for the second 40 years in young, small tree structures. These polygons start

with an average severity of 3.8 and end with an average of 4.8. Both averages are high for young-tree structure, but the increase is indicative of the potential for the root pathogens to maintain a very long-term hold on these sites, stalling stand development indefinitely. The outcome of this function can be seen in the trend toward a higher frequencies of extremely high root disease severity levels (Table 6.38).

The way in which root disease functions depends to a large extent on the intensity of disease in a stand. In both ecosections, there is a gradual increase in the extremely high severities. For example, in M332a, the frequency of severity classes 6-8, indicating at least 50 percent canopy loss from root disease, was a little more than 8 percent of hectares in the 1975-era survey but is expected to increase by a few percent by 2015, to something closer to 11 percent. With this trend, an increase in the stalling function, in which polygons remain long-term in structure classes 1 or 2, is expected to increase.

Table 6.38: Trends in frequencies of root disease severity levels for the subsample consisting of polygons surveyed in both the 1935 and 1975 eras.

	M332a (6314.6 hectares)			M333d (22,006.2 hectares)		
Root Disease Severity Rating	**1935 era**	**1975 era**	**2015 projected**	**1935 era**	**1975 era**	**2015 projected**
0	.02	.02	.00	.07	.01	>.01
1	.09	.03	.03	.17	.09	.05
2	.34	.25	.21	.29	.23	.12
3	.24	.26	.18	.28	.23	.26
4	.10	.20	.29	.16	.22	.32
5	.16	.16	.18	>.01	.12	.16
6	.03	.05	.08	.03	.05	.07
7	.00	.01	.02	>.01	.04	.03
8	.00	.01	.01	>.01	.01	.01

The overall trends in root disease severity from the 1935 era to the 1975 era saw fairly large increases in M333d and more modest increases in M332a (Table 6.39). This trend appears likely for the 40 years after the 1975 era as well. Habitat type groups 2 and 4 show particularly large probable increases in root disease severity through 2015 for the two ecosections combined. In both of these habitat type groups, an accumulation of Douglas-fir and grand fir cover types have occured and appear likely to increase in the future. Expansion and of root disease patches and intensification of tree mortality in afflicted stands is a reasonable expectation given this trend in cover types.

Table 6.39: Trends in root disease severity by habitat type group from the the 1935 era (calculated by polygon class) to the 1975 era (measured) for polygons surveyed in both time periods, and projected disease severity in 2015 based on probable polygon class changes from 1975 to 2015.

	M332a (6,314.8-hectare subsample)			M333d (20,006.2-hectare subsample)		
HT Group	1935	1975	2015	1935	1975	2015
1	2.2	2.2 (0)	2.6 (+0.4)*	1.5	2.2 (+0.7)	2.4 (+0.9)
2	1.5	2.1 (+0.6)	3.5 (+2.0)	2.5	4.0 (+1.5)	4.2 (+1.7)
3	3.8	3.9 (+0.1)	4.0 (+0.2)	2.3	4.4 (+1.1)	4.6 (+1.3)
4	3.0	4.5 (+1.5)	5.1 (+2.1)	2.6	3.8 (+1.2)	3.9 (+1.3)
5	4.3	4.8 (+0.5)	5.0 (+0.2)	2.5	3.0 (+0.5)	3.7 (+0.7)
6*	3.0	3.0 (0)	2.7 (-0.3)	1.0	2.0 (+1.0)	2.6 (+1.6)
7	3.5	3.8 (+0.3)	4.1 (+0.3)	2.4	3.6 (+1.2)	3.9 (+1.5)
8*	2.0	2.6 (+0.6)	2.9 (+0.3)	0.0	3.0 (+3.0)	3.0 (+3.0)
9	2.7	2.9 (+0.2)	2.8 (-0.1)	2.3	3.5 (+1.2)	3.5 (+1.2)
10	1.6	2.0 (+0.4)	2.0 (0)	2.4	4.4 (+2.0)	2.9 (+0.5)
11**	0.0	0.0 (0)	0.0 (0)	0.3	1.8 (+1.5)	2.0 (+1.7)
15**	na	na	na	0.5	2.8 (+2.3)	6.4 (+5.9)
All HTs	2.8	3.2 (+0.4)	3.6 (+0.4)	2.4	3.4 (+1.0)	3.8 (+1.4)

* Cumulative change in root disease severity

** Sample sizes were too small in these habitat type groups to confer significance to these trends.

The gradual increase in root disease severity indicated in this analysis is consistent with observations recorded in northern Idaho over the past two decades. Numerous reports of this phenomenon have associated apparent increases in root disease severity with replacement of early-seral tree species, particularly western white pine (Byler et al. 1995, Monnig and Byler 1992), ponderosa pine, and western larch (Monnig and Byler 1992), by Douglas-fir and grand fir. The combined effects of white pine blister rust, fire exclusion, and selective harvest are thought to account for these changes in species composition.

DOUGLAS-FIR BEETLE SUCCESSION FUNCTIONS

by Sandra Kegley

Introduction

The Douglas-fir beetle, a native bark beetle, has coevolved with its host, Douglas-fir, for thousands of years. The beetle acts as a recycling agent, killing mature trees and providing room for younger trees to grow. The Douglas-fir beetle is not a particularly aggressive bark beetle and it prefers to infest trees with little natural resistance, such as windthrown trees, those scorched by fire, infected with root diseases, defoliated by western spruce budworm or Douglas-fir tussock moth, or weakened by drought. Mature, larger-diameter trees are also preferred. Beetle populations can increase when there is a large amount of these weakened trees available and resultant populations can attack and overcome apparently healthy trees. Outbreaks occur in forests dominated by mature Douglas-fir, and can be quite dramatic. Patches as large as 500 trees can be attacked and killed in one year. Beetles produce less offspring in healthy trees, and outbreaks rarely persist more than 2-4 years.

Weeding Function

When beetle populations are low or in forests containing minor amounts of Douglas-fir, the beetle will seek out and attack the larger-diameter Douglas-fir, particularly those weakened by other agents, effectively weeding out the mature trees. On Douglas-fir habitat types in a seral condition where there is a majority of ponderosa pine, lodgepole pine, or western larch, and minor amounts of Douglas-fir, the affect of the beetle would be to remove the Douglas-fir and maintain the other seral species. On Douglas-fir habitat types in a climax condition with Douglas-fir the dominant tree species, the loss of scattered small groups or individual mature Douglas-fir would create openings, changing from a closed-canopy structure class (SC 3) to an open canopy (structure class 4). On grand fir, western hemlock, cedar, subalpine fir, and mountain hemlock habitat types where Douglas-fir is seral, the Douglas-fir beetle would create openings for the more shade-tolerant species to grow, pushing the forest to a faster climax condition.

Group-killing Function

Douglas-fir outbreaks are most often triggered by an event such as windthrow. Low-intensity fire or defoliator outbreaks may also create a large amount of Douglas-fir with little or no resistance to beetle attack. Beetle populations increase rapidly in these weakened or downed trees and subsequent generations attack and kill standing green trees. The most susceptible stands contain a large proportion of Douglas-fir that is at least 120 years old and at a density of at least 80 percent normal stocking for the site (generally above 240 square feet per acre) (Furniss et al. 1979, 1981). Younger stands (80-120 years old) become susceptible as density increases. An increase in density, as well as age, is linked to a decline in growth and host resistance which increases susceptibility. In northern Idaho, data from one very large outbreak on the Clearwater National Forest, which was triggered by trees fallen during clearing for Dworshak Reservoir, suggest that the most susceptible stands are located in grand fir and western red cedar habitat types where Douglas-fir grows most productively (Furniss et al. 1979, 1981). Susceptible stands may also occur in drier grand fir or Douglas-fir habitat types, but only on those moist enough to support closed stands. Other factors, such as drought, root disease, and defoliation, can increase

forest susceptibility. Patches of 50-150 trees are commonly killed during outbreaks, but patches can occasionally reach as many as 200-500 infested trees. The frequency and extent of outbreaks is dependent upon unpredictable windthrow events, low-intensity fires, or defoliator outbreaks, and has varied over time for different geographic areas. However, for our analysis, we are assuming an outbreak trigger event occurs at least once every decade. In ecosections M332a and M333d, outbreaks of western spruce budworm and Douglas-fir tussock moth have had a much greater affect on true firs than on Douglas-fir. Defoliator outbreaks are probably not a major trigger for Douglas-fir beetle outbreaks in these ecosections as they are elsewhere in Region 1 and in other parts of western North America.

During an outbreak, on Douglas-fir habitat types, the Douglas-fir beetle would most often attack stands in mature closed-canopy structure class (structure class 3). When small groups of mature Douglas-fir are killed, openings are created in the forest canopy, changing forest structure to a structure class 4 (Figure 6.33). When large groups of Douglas-fir are killed, the openings allow smaller trees to grow, resetting succession to a seedling, sapling, or pole stage (structure classes 1 or 2). Forest type may change from Douglas-fir to pines or larch if there is an abundance of seral species in the stand.

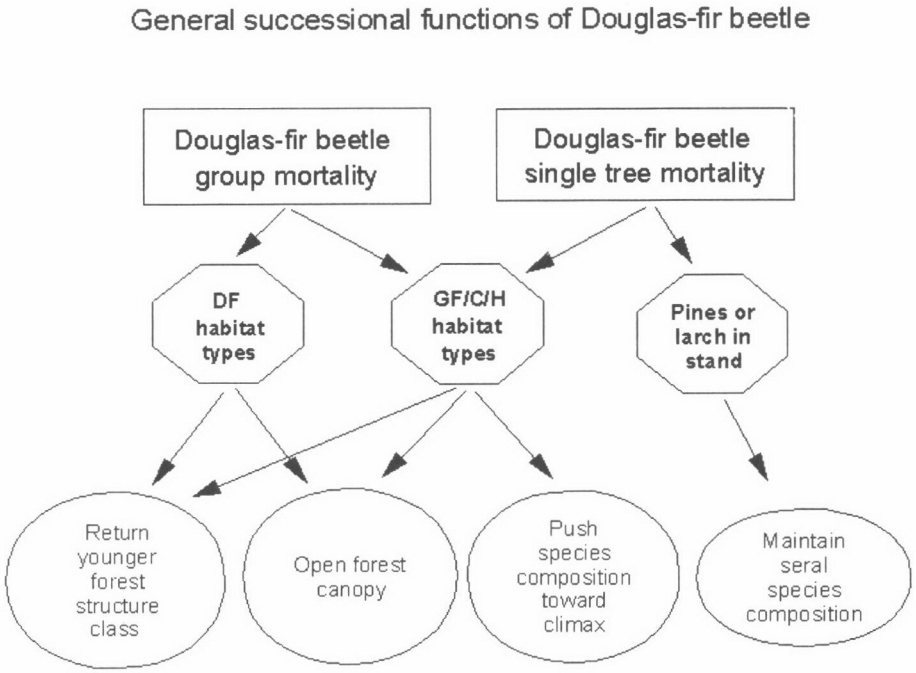
General successional functions of Douglas-fir beetle
Douglas-fir beetle group mortality
Douglas-fir beetle single tree mortality
DF habitat types
GF/C/H habitat types
Pines or larch in stand
Return younger forest structure class
Open forest canopy
Push species composition toward climax
Maintain seral species composition

Figure 6.33: General succession functions of Douglas-fir beetle.

On grand fir, cedar, western hemlock, and mountain hemlock habitat types, the Douglas-fir beetle would also most often attack stands in mature closed canopy structure class (Figure 6.33). Openings created would allow more shade-tolerant tree species to grow, pushing the forest toward a faster climax. Small openings would change forest structure to an open forest canopy. Larger openings may change forest structure to a seedling, sapling, or pole structure classes.

The Douglas-fir beetle may also affect stands in structure class 4 on all habitat types. Beetle activity could keep the forest in structure class 4 (prevent closure) by continually creating

openings in the forest canopy or reset succession to a structure class 1 or 2. Occasionally Douglas-fir beetle could also affect stands in structure class 2, especially where there are at least some large-diameter trees in the stand. Their affect most likely would be to remove the Douglas-fir and open the forest canopy (Figure 6.33).

Mortality caused by Douglas-fir beetle may also predispose a forest to fire, allowing new seedlings to become established. Stand-replacing fires favor seral species and reset forest succession.

Statistics from M332a

High and moderate group Douglas-fir beetle API values and weeding functions occurred across habitat type groups 1, 2, 3, 4, 5, 7, and 9, on forest types DF, PP, LP, GF, L, S, C, MH, AF, and various combinations of those forest types, and in structure classes 2, 3, and 4. The highest group API values occurred in Douglas-fir forest types, structure classes 3 and 4. All habitat type group, forest type, structure class combinations (HT/FT/SC) that had a Douglas-fir beetle group API value also had a corresponding Douglas-fir beetle weeding API value. However, there were many HT/FT/SC combinations that had a Douglas-fir beetle weeding function but no group API value. In these HT/FT/SC combinations, there were lesser amounts of large diameter Douglas-fir than where group and weed values occurred together.

High, moderate, and low probability values were assigned to each transition path where Douglas-fir beetle group or weed API values occurred in the starting HT/FT/SC and where the transition could have logically been caused by Douglas-fir beetle. Low probability values were assigned when only a weeding function API value occurred in the starting HT/FT/SC or when the transition was not as logical as others within the same starting HT/FT/SC due to Douglas-fir beetle. Transitions occurring with a low probability due to Douglas-fir beetle included retaining Douglas-fir as the major forest type or changing from a structure class 2 or 4 to a structure class 3 (an increase in density). Moderate or high probability values were assigned based on the proportion of moderate or high group API values in the starting HT/FT/SC. High probability values were only given when there was a high proportion of high API values in the starting HT/FT/SC and the transition was most likely due to Douglas-fir beetle. Transitions most likely due to Douglas-fir beetle include a change in forest type (loss of Douglas-fir component) or a change in structure class to an open forest canopy, or to a younger seedling, sapling, or pole-sized structure class. Twenty percent of the hectares analyzed for transitions in M332a were assigned a high, moderate, or low probability due to Douglas-fir beetle. Of these hectares, 20 percent were rated high, 48 percent moderate, and 32 percent low. These occurred in habitat types groups 1, 2, 3, 5, 7, and 9. The majority occurred in habitat type group 5 (38 percent), group 2 (26 percent) and group 1 (22 percent). The majority of the high probability values occurred in structure class 3 (73 percent) with the remainder in structure class 4 (27 percent). Low and moderate probability values occurred in structure classes 2, 3, and 4.

Transitions occurring in M332a with a high probability due to Douglas-fir beetle occurred on forest types with a Douglas-fir component. On Douglas-fir habitat types, structure class 3, 55 percent changed to a younger structure class but retained a Douglas-fir component; 45 percent retained a Douglas-fir component but changed to a structure class 4 (open canopy). On Douglas-fir habitat types, structure class 4, 100 percent retained a Douglas-fir component but changed to a younger structure class (Figure 6.34). On GF, C, or H habitat types, structure class 3, 86 percent stayed in structure class 3 but lost the Douglas-fir component; the remaining 14 percent retained a Douglas-fir component but changed to an open-canopy structure class (decrease

density). On grand fir, cedar, or western hemlock habitat types, structure class 4, 21 percent lost the Douglas-fir component and stayed in structure class 4 (prevent closure); 46 percent lost the Douglas-fir component and moved to structure class 3; 21 percent lost the Douglas-fir component and changed to an earlier structure class; 12 percent changed to an earlier structure class but retained the Douglas-fir component (Figure 6.35).

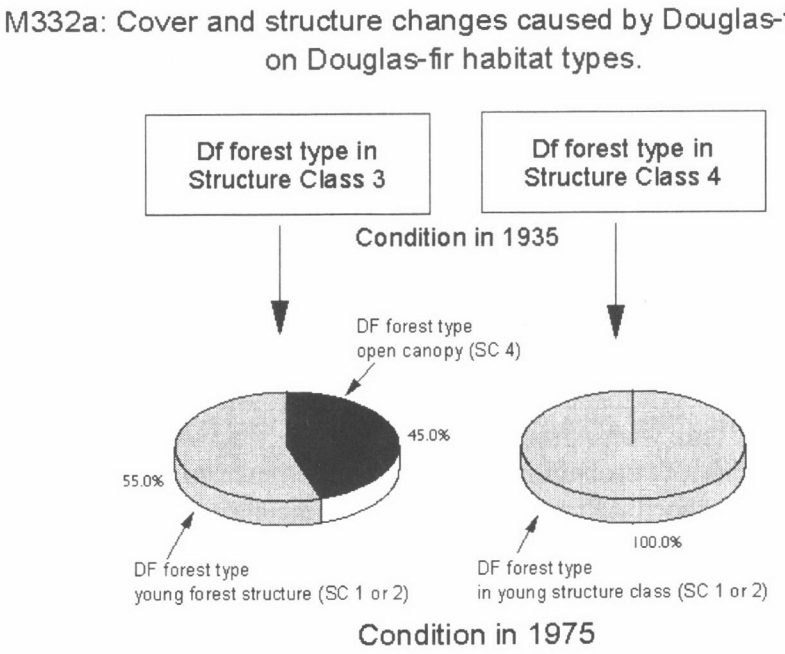
M332a: Cover and structure changes caused by Douglas-fir beetle on Douglas-fir habitat types.
Df forest type in Structure Class 3
Df forest type in Structure Class 4
Condition in 1935
DF forest type open canopy (SC 4)
45.0%
55.0%
100.0%
DF forest type young forest structure (SC 1 or 2)
DF forest type in young structure class (SC 1 or 2)
Condition in 1975

Figure 6.34: Cover and structure changes caused by Douglas-fir beetle on Douglas-fir habitat types, M332a.

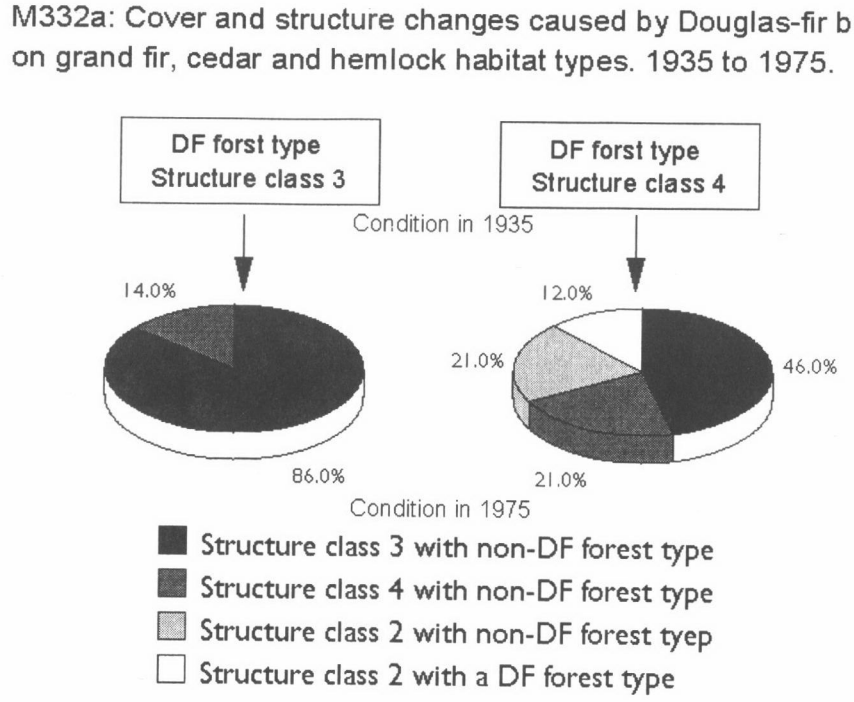
M332a: Cover and structure changes caused by Douglas-fir beetle on grand fir, cedar and hemlock habitat types. 1935 to 1975.
DF forst type Structure class 3
DF forst type Structure class 4
Condition in 1935
14.0%
86.0%
12.0%
21.0%
46.0%
21.0%
Condition in 1975
Structure class 3 with non-DF forest type
Structure class 4 with non-DF forest type
Structure class 2 with non-DF forest tyep
Structure class 2 with a DF forest type

Figure 6.35: Cover and structure changes caused by Douglas-fir beetle on grand fir, cedar, and hemlock habitat types, M332a.

The majority of transitions occurring with moderate probability due to Douglas-fir beetle retained a Douglas-fir component and either kept the forest in an open-canopy structure class (35 percent), changed from a structure class 2 or 3 to an open-canopy structure class (19 percent), or changed to an earlier structure class (19 percent). About 15 percent of the transitions showed a loss of the Douglas-fir component and a change in structure class, and 11 percent stayed in structure class 4 with a loss of the Douglas-fir component.

About 7 percent of the hectares in the M332a sample had low Douglas-fir beetle probability ratings for causing transitions. Most of these indicate a Douglas-fir beetle weeding function. Of these, 63 percent also had a high or moderate probability for root disease. The combination of these two agents increases the likelihood of the transitions occurring. The majority of these transitions resulted in a push to climax species (64 percent) and either prevented canopy closure (52 percent) or changed to an early structure class (23 percent).

Statistics from M333d

Similar to ecosection M332a, Douglas-fir beetle group and weed API values occurred in habitat type groups 1, 2, 3, 4, 5, 7, and 9; forest types DF, PP, C, GF, L, LP, S, AF, WH, WP, MH, and various combinations of those forest types, and structure classes 2, 3, and 4. The highest group API values occurred where Douglas-fir was at least part of the forest type in structure classes 3 and 4. As with M332a, all habitat type group, forest type, structure class combinations that had a Douglas-fir beetle group API value also had a corresponding Douglas-fir beetle weeding function. However, there were many HT/FT/SC combinations that had a Douglas-fir

beetle weeding function without a group API value. In these HT/FT/SC, there were lesser amounts of large-diameter Douglas-fir than where group and weed values occurred together.

There is little historic data in structure class 3 and many transitions with high Douglas-fir beetle API values could not be analyzed in this ecosection. High, moderate, and low transition probabilities were assigned following the same rules as in M332a. In M333d, 11 percent of the total acreage with transition data was assigned a high, moderate, or low probability due to Douglas-fir beetle. Of these, 6 percent was rated high probability, 42 percent moderate probability, and 53 percent low probability. These occurred in habitat types groups 2, 3, 4, 5, 7, and 9. The majority occurred in habitat type group 5 (42 percent), group 4 (19 percent) and group 2 (15 percent). The high probability values for Douglas-fir beetle occurred in structure class 4 (64 percent), structure class 3 (21 percent), with the remainder in structure class 2 (15 percent). Low and moderate probability values occurred almost exclusively in structure classes 2 and 4. These data reflect the low amount of structure class 3 in the historic data base for this ecosection.

High probability transition values for Douglas-fir beetle occurred on habitat type groups 2, 4, 5, and 9. In Douglas-fir mixed species forest types, structure class 2, 100 percent transitioned to structure class 4 (open canopy) with the loss of the Douglas-fir component (Figure 6.36). In Douglas-fir forest type, structure class 3, grand fir, cedar, and western hemlock habitat type groups, 29 percent stayed Douglas-fir but changed to a younger structure class, and 71 percent lost the Douglas-fir component resulting in a push to climax species in the same structure class (Figure 6.36). In Douglas-fir mixed-species forest types, structure class 4, Douglas-fir habitat types, 85 percent went to an earlier structure class, and 15 percent stayed in an open canopy structure class 4 (Figure 6.37). In Douglas-fir mixed-species forest types, structure class 4, grand fir and subalpine fir habitat types, 56 percent resulted in a push to climax in an earlier structure class; and 44 percent lost the Douglas-fir component (push to climax) and stayed in open-canopy structure class 4 (Figure 6.37).

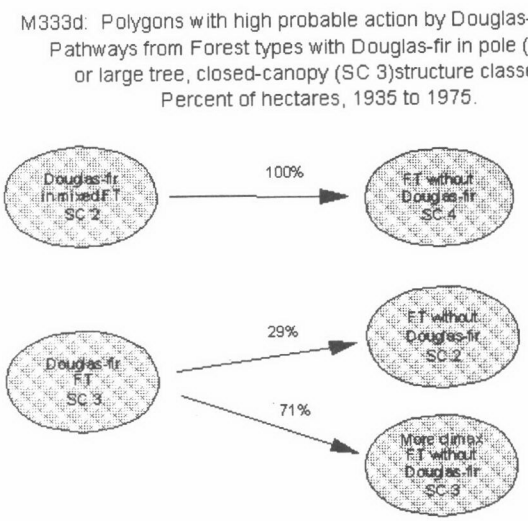
M333d: Polygons with high probable action by Douglas-fir beetle.
Pathways from Forest types with Douglas-fir in pole (SC 2)
or large tree, closed-canopy (SC 3)structure classes.
Percent of hectares, 1935 to 1975.
Douglas-fir in mixed FT SC 2
100%
FT without Douglas-fir SC 4
Douglas-fir FT SC 3
29%
FT without Douglas-fir SC 2
71%
More climax FT without Douglas-fir SC 3

Figure 6.36: Pathways, Douglas-fir forest types in structure classes 2 and 3, high Douglas-fir beetle influence, M333d.

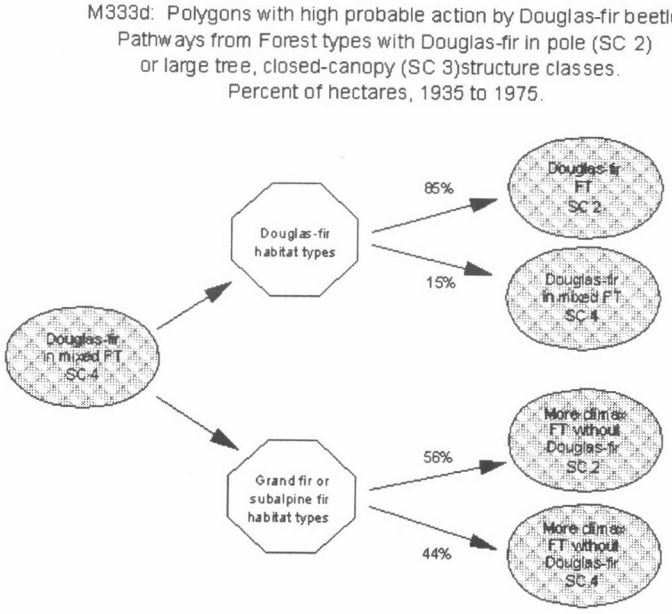
M333d: Polygons with high probable action by Douglas-fir beetle.
Pathways from Forest types with Douglas-fir in pole (SC 2)
or large tree, closed-canopy (SC 3)structure classes.
Percent of hectares, 1935 to 1975.
Douglas-fir in mixed FT SC 4
Douglas-fir habitat types
85%
15%
Douglas-fir FT SC 2
Douglas-fir in mixed FT SC 4
Grand fir or subalpine fir habitat types
56%
44%
More climax FT without Douglas-fir SC 2
More climax FT without Douglas-fir SC 4

Figure 6.37: Pathways, Douglas-fir forest types in structure class 4, high Douglas-fir beetle influence, M333d.

Most moderate probability transition values for Douglas-fir beetle were assigned to transitions from a structure class 2 to an open canopy structure class 4 (34 percent). About 24 percent changed from a structure class 4 to a younger structure class, and 29 percent stayed in a structure class 4. On 46 percent of the area with moderate transition probabilities, there was a loss of Douglas-fir component (Figure 6.38).

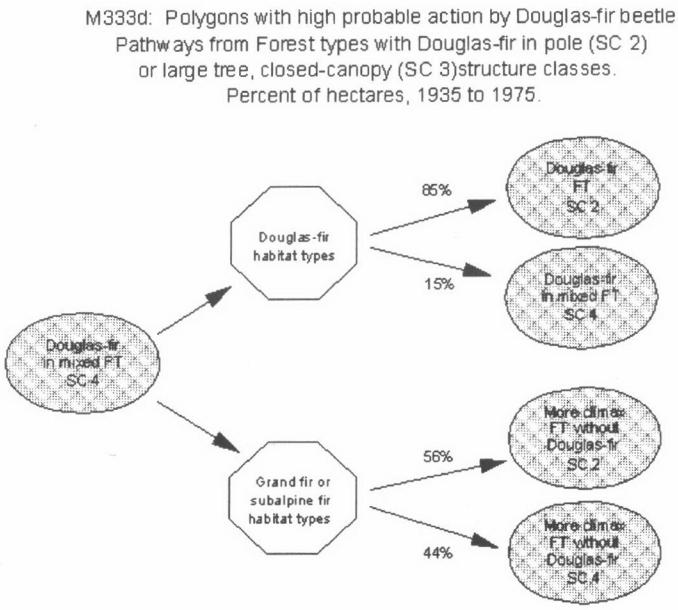
M333d: Polygons with high probable action by Douglas-fir beetle.
Pathways from Forest types with Douglas-fir in pole (SC 2)
or large tree, closed-canopy (SC 3)structure classes.
Percent of hectares, 1935 to 1975.
Douglas-fir in mixed FT SC 4
Douglas-fir habitat types
85%
15%
Douglas-fir FT SC 2
Douglas-fir in mixed FT SC 4
Grand fir or subalpine fir habitat types
56%
44%
More climax FT without Douglas-fir SC 2
More climax FT without Douglas-fir SC 4

Figure 6.38: Pathways, Douglas-fir forest types in structure class 2 and 3, high Douglas-fir beetle influence, M333d.

The largest amount of area with a Douglas-fir beetle probability value was assigned low probability in this ecosection. These indicate a possible transition due to Douglas-fir beetle most likely resulting from Douglas-fir beetle weeding functions. Seventy-seven percent of the hectares with low Douglas-fir beetle transition probabilities also had a moderate or high root disease probability. The majority of the transitions that occurred with low Douglas-fir beetle and moderate or high root disease affected cover by pushing to climax (75 percent). Most of these transitions affected structure by either preventing closure (38 percent) or changing to an earlier structure class (26 percent).

Overall status within the sample

Transitions attributed to Douglas-fir beetle with a high, moderate, or low probability in M332a covered 20 percent of the area sampled that contained both current and historic data. This was about twice the amount covered in ecosection M333d. In M333d, 11 percent of the total transition area was assigned high, moderate, or low probabilities due to Douglas-fir beetle. However, Douglas-fir beetle probabilities occurred on 44 percent of the forest types with a Douglas-fir component in structure classes 3 and 4 in M333d. Those forest types and structure classes covered 16 percent of the total M333d sample area.

Comparisons Between M332a and M333d

The transitions that occurred due to Douglas-fir beetle were very similar in the two ecosections. Douglas-fir forest types in structure class 3 went to an open canopy, an earlier structure class, or changed forest type to a more climax species in both ecosections. Douglas-fir forest types in structure class 4 went to an earlier structure class, stayed an open canopy, or lost the Douglas-fir component. Differences occurred between the two zones in that high probabilities were assigned in Douglas-fir forest types, structure class 2 in M333d but not in M332a,

although this covered only a small amount of area. The proportion of area potentially affected by Douglas-fir beetle also differed. The area with Douglas-fir beetle transition probabilities covered almost twice the sample area of M332a than of M333d. Ecosection M333d had less Douglas-fir in structure class 3 (the most likely forest type/structure class combination to support Douglas-fir beetle activity) in the historic sample than M332a.

Ecological Implications

The most common transitions that occurred due to a high probability of Douglas-fir beetle were a change in forest type, most often to a climax species; and a change in forest structure to a younger structure class or to an open forest canopy with low density. There were only a few cases where Douglas-fir beetle actions maintained other seral species but these had low or moderate probabilities.

Functions of Douglas-fir beetle weeding and group killing actions were similar but differ in magnitude of the result. Douglas-fir beetle group killing functions resulted in higher probabilities for transitions to occur than did the weeding functions by themselves. This is partly because the loss of large groups of mature trees will cause a faster and more noticeable transition than the loss of individual mature trees over a longer time period. Douglas-fir beetle weeding functions will be expressed to a greater degree when looking at the interaction between Douglas-fir beetle and root disease (see ecosections on root disease functions and significant combinations of agents). The transition pathways that were assigned a low probability for Douglas-fir beetle were most likely where a weeding function occurred without a group Douglas-fir beetle probability. The majority of these low probability Douglas-fir beetle transitions had a high or moderate probability for root disease. The combination of the two agents will increase the probability of the transition occurring. Although not as dramatic as a group killing action, Douglas-fir beetle weeding with root disease will cause significant changes over the landscape over time.

Douglas-fir beetle will continue to be a major agent of change across Douglas-fir forest types during the next 40 years in these ecosections. Douglas-fir beetle activity may increase in frequency as our sample data show an increase in the amount of Douglas-fir forest types currently compared to 40 years ago. In ecosections M333d and M332a, 40 percent and 46 percent respectively, of the current data were Douglas-fir forest types or Douglas-fir mixed with other species forest types in structure classes 2, 3, and 4. These are the types most likely to support Douglas-fir beetle activity.

MOUNTAIN PINE BEETLE IN LODGEPOLE PINE: SUCCESSION FUNCTIONS

By Carol Bell Randall

The mountain pine beetle, *Dendroctonus ponderosae* Hopk., is a native bark beetle whose depredations can have major impacts on succession in ecosystems with lodgepole pine. Successful mountain pine beetle attacks kill lodgepole pine.

Not all lodgepole pine trees are equally likely to be successfully attacked. Mature, large-diameter (and thick phloem) trees receive the most attacks in a given stand. Some trees within a given size and age class are able to resist beetle attacks. As trees become older than about 50 years, the proportion of trees in a given stand able to resist beetles, if attacked, generally decreases with tree age. The beetles attack the lodgepole pines of largest diameter each year of the infestation until mostly small diameter lodgepole pines remain when the infestation stops.

In some areas mountain pine beetle populations persist for many years in small pockets, doing damage to only a few trees in the stand. In other situations, mountain pine beetle has exploded from an endemic state to outbreak conditions in about 5 years, and these outbreaks have killed lodgepole pine over hundreds of thousands of acres. Outbreaks in even age stands of old trees of the same diameter class kill almost all trees, whereas mixed age stands lose mostly the larger trees (Amman et al. 1977).

Succession Functions of the Mountain Pine Beetle as Related to the Successional Role of Lodgepole Pine

Most lodgepole pine forests were established as a result of fire, particularly in the Rocky Mountains. Throughout post-glacial periods, recurrent fires that sometimes covered extensive areas probably hindered the development of climax forests and favored lodgepole pine (Brown 1975). Some generalizations about how lodgepole pine will interact with other tree species and what types of disturbances it may encounter may be made by considering the habitat type of the site. By knowing the habitat type of a site, it is possible to determine the successional role that lodgepole pine is likely to play (Pfister and Cole 1985; Volland 1985; Amman 1977). Depending on lodgepole's successional role and its abundance in a stand, the impact of disturbance agents such as the mountain pine beetle on stand structure and composition may be predicted (Amman 1977).

There are four commonly recognized successional roles for lodgepole pine: minor seral, dominant seral, climax, and persistent (Pfister and Daubenmire 1975). Mountain pine beetle may be found killing lodgepole pine in any of these roles. The beetles' impact on lodgepole pine does not usually result in an alteration of stand succession unless lodgepole pine is a major stand component (Figure 6.39).

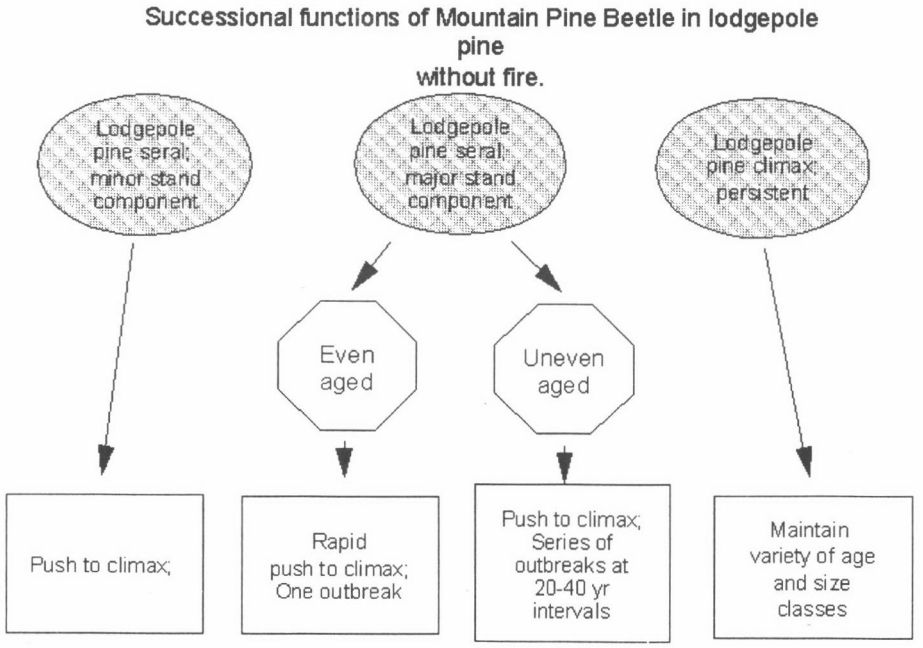
Successional functions of Mountain Pine Beetle in lodgepole pine without fire.
Lodgepole pine seral; minor stand component
Lodgepole pine seral; major stand component
Lodgepole pine climax; persistent
Even aged
Uneven aged
Push to climax;
Rapid push to climax; One outbreak
Push to climax; Series of outbreaks at 20-40 yr intervals
Maintain variety of age and size classes

Figure 6.39: Succession functions of mountain pine beetle in lodgepole pine without fire.

Lodgepole pine as minor seral

Where lodgepole pine is a minor seral component of the stand, the succession function of the mountain pine beetle is to accelerate succession. Where it plays a minor seral role, lodgepole pine is most commonly a minor component of young, even-age, mixed-conifer stands. It is replaced by shade-tolerant associates in 50 to 200 years; the more mesic the site, the sooner replacement occurs. On some habitat types where lodgepole plays a minor seral role, fire has allowed the species to dominate a stand. In these situations, the lodgepole overstory tends to open up within 100 to 120 years, allowing succession to more shade-tolerant species to progress.

The impact of the mountain pine beetle as an accelerant of stand succession may be relatively small depending upon the proportion of lodgepole in the stand. Other species in the stand replace lodgepole pine more rapidly than if the mountain pine beetle had not been active; however, succession in these stands usually proceeds in a rapid manner regardless of mountain pine beetle activity. Other insect and disease agents may play a more significant role in accelerating stand succession on these sites than mountain pine beetle. In areas of the St. Joe National Forest, pure lodgepole pine stands on minor seral habitat types are beginning to open up; however, root disease and stem cankers appear to be driving the process; not mountain pine beetle (Bell Randall and Byler 1997).

Lodgepole pine is often a minor seral on warm-dry Douglas-fir, cool-moist grand fir/ hemlock/cedar, and cold subalpine fir/mountain hemlock habitat type groups.

Lodgepole pine as dominant seral

On habitat types where lodgepole pine is a dominant seral species, the function of the mountain pine beetle is also to accelerate succession. Lodgepole pine is often the dominant

forest type of even-age stands in these habitat types. Often, the lodgepole forests occurs with a vigorous understory of shade-tolerant species that will replace lodgepole in 100 to 200 years. Succession occurs most rapidly where lodgepole pine and shade-tolerant associates become established simultaneously. Lodgepole pine gains dominance through rapid early growth, but shade-tolerant species persist and assume dominance as lodgepole pines die.

In dominant seral stands the mountain pine beetle hastens the stand towards climax by releasing under story species such as Douglas-fir in some habitat types; grand fir, western hemlock, or western red cedar in others; and subalpine fir and Engelmann spruce in still others. Depending on the nature of the lodgepole stand, the mountain pine beetle may remove the vast majority of lodgepole in one infestation, or it may remove the lodgepole over time through a series of infestations. In susceptible, even-aged lodgepole stands, e.g. all of the trees are approximately the same size (8"or greater average diameter) and age (80 years or older), a mountain pine beetle infestation may remove 90 percent + of the lodgepole during one outbreak which may only last for 3 to 5 years. In areas where the lodgepole is more uneven aged, displaying a wide range of age and/ or size classes, mountain pine beetles will kill lodgepole pines of adequate age and phloem thickness (the dominant pines), then will not be active in the stand for another 20 to 40 years until the next cohort of lodgepole reaches susceptibility. This cycle continues until lodgepole is essentially eliminated from the stand.

Lodgepole pine is often a dominant seral on habitat types in the spruce, dry Douglas-fir, and cold subalpine fir habitat type series.

Lodgepole pine as persistent and/or climax

In stands where lodgepole pine plays a persistent successional role, it forms the dominant forest type of the stand with little evidence of replacement of shade tolerant species. The shade tolerant species occur only as scattered individuals and apparently are too few and lack sufficient vigor to replace lodgepole pine. Lodgepole pine maintains dominance either because of inadequate seed source for potential competitors or because the sites are poorly suited for other species. Where lodgepole is climax it is the only species capable of growing and self perpetuating on the site. Usually these sites occur in frost pockets or on areas where the soil is not capable of supporting other species.

Lodgepole pine persists long enough in these stands for a number of mountain pine beetle infestations to occur. Mountain pine beetle infestations are almost chronic on many of these sites. The forest will consist of trees of different sizes and ages ranging from seedlings to a few over-mature individuals. In these forests the beetle infests and kills most of the lodgepole pine as they grow to larger sizes. Openings created in the stand as a result of the largest trees being killed are seeded by lodgepole pine (Figure 6.39). The cycle is then repeated as other lodgepole pines reach sizes and phloem thicknesses conducive to increases in beetle populations. The result is 2 or 3 story stands consisting of trees of different ages and sizes. A mosaic of small clumps of different ages and sizes may occur. The overall effect is likely to result in more infestations by the beetle because of the consistent source of food. Beetle infestations in such forests may kill fewer trees per acre in each infestation than would occur in even aged stands developed after fire and in those where lodgepole pine is seral (Amman 1977).

Lodgepole pine is often persistent or climax on some cold-dry subalpine fir habitat types and on the entire lodgepole pine series.

Mountain pine beetle, fire, and succession

Fire, more than any other single factor, is responsible for the establishment and structure of most of the lodgepole forests we know today (Brown 1975). Mountain pine beetle epidemics, by killing lodgepole pine and creating fuels, impact fire regimes (Figure 6.40). The interactions of fire and mountain pine beetle are inextricable in most lodgepole pine forests (Crane and Fisher, 1986).

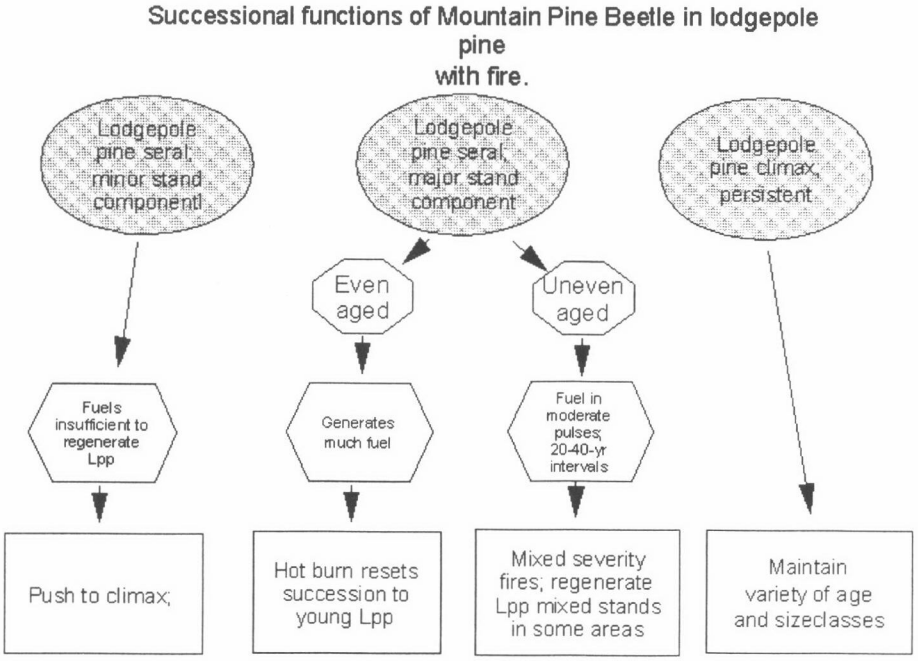
Successional functions of Mountain Pine Beetle in lodgepole pine with fire.
Lodgepole pine seral, minor stand component
Lodgepole pine seral, major stand component
Lodgepole pine climax, persistent
Even aged
Uneven aged
Fuels insufficient to regenerate Lpp
Generates much fuel
Fuel in moderate pulses; 20-40-yr intervals
Push to climax;
Hot burn resets succession to young Lpp
Mixed severity fires; regenerate Lpp mixed stands in some areas
Maintain variety of age and sizeclasses

Figure 6.40: Succession functions of mountain pine beetle in lodgepole pine with fire.

Where lodgepole pine is seral, forests are perpetuated through the effects of periodic fire (Tackle 1964). Moderate to heavy fuel loads are much more likely to occur in seral stands of lodgepole pine than in climax stands in central Idaho (Crane and Filcher 1986). Large accumulations of dead material caused by periodic beetle infestations result in very hot fires when they do occur (Brown 1975). Hot fires of this nature eliminate Douglas-fir, which otherwise is more resistant to fire damage than lodgepole pine and other shade-tolerant species, resulting in a return to a pure lodgepole pine forest. These fires would completely eliminate the beetles' food supply from vast acreages for many years while the entire stand of trees grow from seedlings to sizes conducive to beetle infestation. Where beetle infestations do not generate such high fuel loadings hot fires are not as likely. The light surface fires consistent with this level of fuel loading would not be adequate to kill large, thick barked Douglas-fir and return lodgepole pine to the dominant position in the stand. If succession progresses beyond a point where there is a lodgepole pine component, it is unlikely that lodgepole pine seed would be available to seed in after a fire except along edges where forests with lodgepole as a seral species join forests where lodgepole is a persistent or climax species.

Fires in persistent and climax lodgepole pine forests should not be as hot as those where large epidemics of beetles have occurred. Smaller, more continuous deposits of fuel are

available on the forest floor. The lighter beetle infestations, and thus lighter accumulations of fuel, would result in fires that would eliminate some of the trees but probably would not cause total regeneration of the stand. This is more beneficial to the beetle because a more continuous supply of food would be maintained.

Mountain Pine Beetle in Lodgepole Pine in Northern Idaho

Cover type analysis for mountain pine beetle in lodgepole pine in M332a: API analysis

In the 1975-era data for M332a there were 16 habitat type group/cover type/structure class combinations (polygon classes) which had calculated mountain pine beetle in lodgepole pine API values. These combinations occurred in habitat type groups 1, 2, 3, 4, 7, 9, and 10 with cover types 2, 5.2, 7, 9, and 11. The most frequent successional role of lodgepole pine was dominant seral.

Nine of the 16 polygon classes were represented in the historic data. Seven of these classes had a lodgepole pine cover type 7 (lodgepole pine greater than 50 percent). For these seven classes, the observed transitions were consistent with mountain pine beetle activity impacts upon succesion; that is, the cover type changed to one with less lodgepole (Figure 6.41) and/or the structure class was stalled, moved to an earlier structure class (1 or 2), or was opened up (becoming a SC 4) (Figure 6.42).

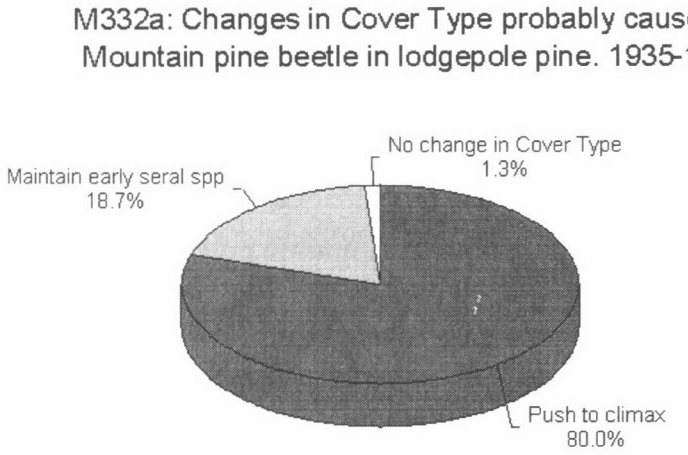

Figure 6.41: Changes in cover type probably caused by mountain pine beetle in lodgepole pine, M332a.

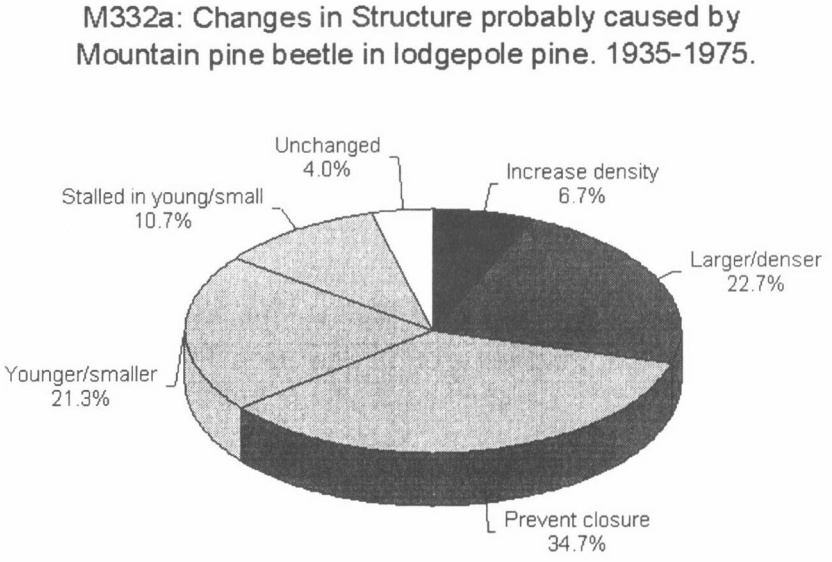

Figure 6.42: Changes in structure probably caused by mountain pine beetle in lodgepole pine, M332a

The transitions in the remaining two classes are more difficult to characterize in terms of mountain pine beetle impacts on succession. One polygon class (HT 7/CT 11/SC 3) stalled and was still HT 7/CT 11/SC 3 in the 1975 era. Within this polygon class in the 1975-era sample, only 5 percent of the area had a mountain pine beetle in lodgepole pine API value indicating that only 5 percent of the area in this class contained more than 20 percent lodgepole pine. On that 5 percent of the area, however, mountain pine beetle in lodgepole pine API values were high indicating that stand conditions were highly conducive to mountain pine beetle. The mountain pine beetle could have been actively removing the lodgepole pine present in the stands. This activity, however, would not result in a CT change, so would not result in a detectable successional change.

The final polygon class with calculated mountain pine beetle in lodgepole pine API values in the 1975 era represented in the 1935-era sample was HT 3/CT 9.2/SC 4. This polygon class transitioned to HT 3/CT 9/SC 4. In the 1975-era sample, only 25 percent of the hectares in this class received an mountain pine beetle in lodgepole pine API rating indicating only 25 percent of the hectares contained more than 20 percent lodgepole. This 25 percent of the area received a high mountain pine beetle in lodgepole pine API, indicating that stand conditions were highly conducive to mountain pine beetle activity. Mountain pine beetle would remove lodgepole, aiding the establishment of more climax species, witnessed in the cover type change from 9.2 (GF less than 50 percent) to 9 (C/GF greater than 50 percent), however the impact of mountain pine beetle on lodgepole in the observed transition is not obvious because the cover type designations do not definitively say that lodgepole pine was present.

Observed transitions in lodgepole pine cover types (7) from 1935 to 1975 eras

There were 44 observed transitions in polygon classes that had a lodgepole pine cover type in the 1935 era. At that time, 1,101 hectares had a lodgepole pine cover type. In the 1975-era, only 554 hectares, approximately half the 1935-era level, had a lodgepole pine cover type. All of the hectares in lodgepole pine cover types in the 1975 era were in lodgepole cover types in the 1935 era; i.e. no lodgepole cover types were recruited from other cover types. Of the 1,101 hectares of lodgepole pine in the 1935 era, 50 percent (554 hectares) stayed in lodgepole pine cover types; 27 percent (296 hectares) transitioned to subalpine fir, mountain hemlock or white-bark pine cover types; 10 percent (115 hectares) became Douglas-fir cover type and minor amounts became spruce, grand fir, cedar, or ponderosa pine cover types.

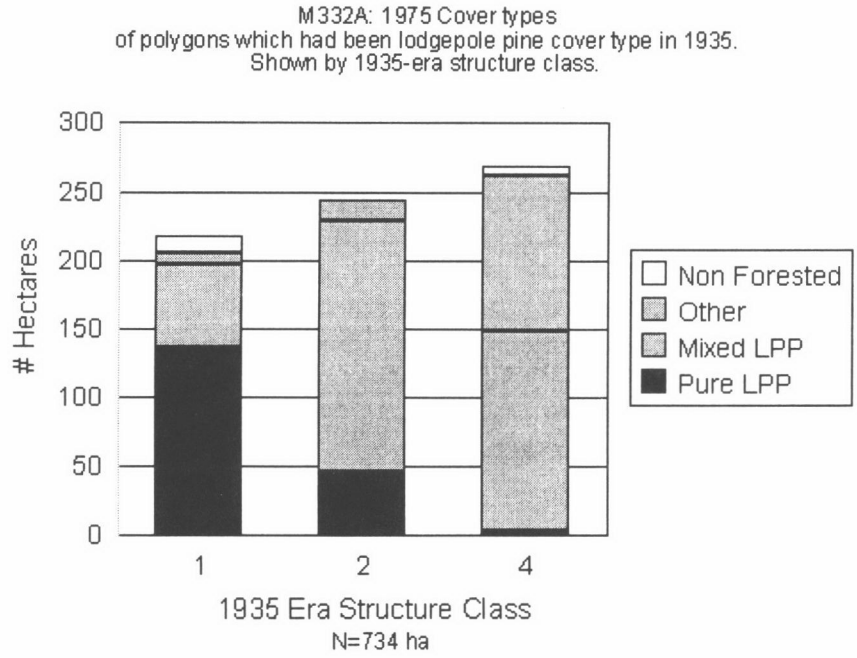

Figure 6.43: Polygons of 1975-era cover types having lodgepole pine cover type in the 1935 era, M332a.

There were dramatic changes in the structure class distribution of lodgepole pine cover types from the 1935 era to the 1975 era. In the 1935 era, approximately 25 percent (271 hectares) of lodgepole pine cover types were in structure class 1, 49 percent (544 hectares) were in structure class 2; and 26 percent (286 hectares) were in structure class 4 (Figure 6.44). In the 1975, era 85 percent of forests with lodgepole pine cover types were in structure class 2 (473 hectares); 10 percent (56 hectares) were in structure class 3; 4 percent (20 hectares) were in structure class 1; and 1 percent (5 hectares) was in structure class 4.

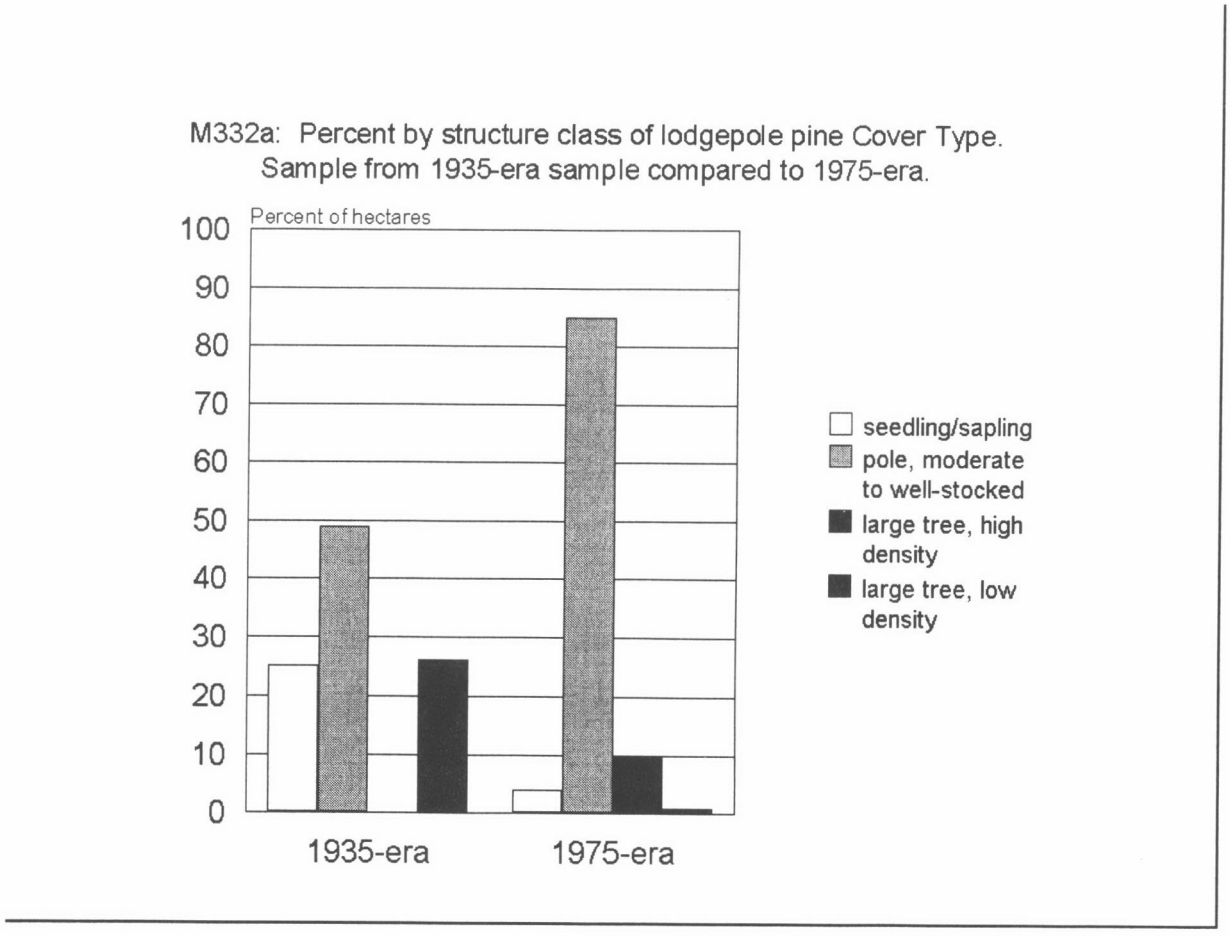

Figure 6.44: Percentage of lodgepole pine cover type by structure class, 1935 era to 1975 era, M332a.

Most of the transitions in lodgepole pine cover type in the 1935 era were consistent with mountain pine beetle activity (Table 6.40). In terms of area, half the lodgepole pine cover type in the 1935-era sample transitioned to a different cover type, indicating that lodgepole pine abundance was reduced, potentially by mountain pine beetle activity. Twenty-nine percent of the sample (315 hectares) stalled; i.e., succession did not move forward. This is consistent with mountain pine beetle activity removing larger-diameter trees, preventing stands from changing structure classes. In 2 percent of hectares of the 1935-era lodgepole pine cover type, structure class changes were consistent with mountain pine beetle activity removing larger trees, thus creating openings or moving the structure class back.

The remaining 19 percent of the 1935-era lodgepole pine cover type hectares (212 hectares) experienced transitions which were contrary to what would be expected if mountain pine beetle was active. On these hectares, either the mountain pine beetle was not active or its impacts were overshadowed by other disturbance factors.

Table 6.40: Transitions by cover type in M332a with the potential for mountain pine beetle lodgepole pine activity.

Number of Transitions	Successional Impact	Notes on Transition
30	Change in cover type	Mountain Pine Beetle activity may have resulted in the change from a lodgepole pine cover type to another cover type with less lodgepole pine
5	No successional change observed: stalled	Mountain pine beetle activity may have prevented succession from moving forward by removing larger lodgepole pine and preventing canopy closure.
4	No change in cover type but a change in Structure class	In three of these transitions, the structure class moved from a 4 to a 1 or 2. Mountain pine beetle may have facilitated this by removing the remaining larger diameter lodgepole pine resulting in a structure class shift. In one transition, the structure class moved from a 2 to a 4. Mountain pine beetle may have facilitated this by creating openings in the canopy, preventing closure.
5	Successional changes contrary to what would be expected if mountain pine beetle was active	Either the mountain pine beetle was not active in these transitions or its impacts were overshadowed by other factors, such as succession or other disturbance agents.

Conclusions for M332a based on cover type analysis

Cover type analysis indicated a 50 percent reduction in the number of hectares occupied by lodgepole pine cover types from the 1935 era to the 1975 era. The cover type analysis also indicated that lodgepole pine cover types were not recruited from other cover types. There was also a significant shift in the structure class composition of lodgepole pine forest types from the 1935 era to the 1975 era. In the 1935 era, approximately half of the lodgepole pine cover types were structure class 2, and one fourth in each of structure classes 1 and 4. By the 1975 era, the proportion of lodgepole pine cover types in structure class 2 had increased to 85 percent, 10 percent were in structure class 3, 4 percent in structure class 1, and 1 percent in structure class 4. The changes in amount of lodgepole pine cover type and relative proportion of structure classes are likely the result of lack of fire and mountain pine beetle activity between the 1935 era and the 1975 era.

The successional stage changes observed between the 1935 era and the 1975 era indicate that, on the hectares of lodgepole pine cover type remaining in the 1975 era, there is less diversity in structure than there had been in the 1935 era so there is a higher likelihood that the majority of lodgepole cover types will become susceptible to mountain pine beetle at the same time. Stands in structure class 3 are the most prone to mountain pine beetle activity, though susceptibility may begin in the later portion of structure class 2. In the 1975 era, 85 percent of the remaining lodgepole pine cover types were in a structure class 2.

Forest Type Analysis for Mountain Pine Beetle in Lodgepole Pine in M332a

API analysis

Action probability index (API) data could be calculated for 20 of the 26 HT/FT/SC combinations occurring in the 1935-era data. Eleven of the 20 combinations contained high or moderate mountain pine beetle API, even though two combinations did not have lodgepole pine in the forest type definition (i.e., lodgepole pine did not comprise more than 30 percent of the canopy cover). A high API value for a non-lodgepole pine forest type indicates that there are susceptible lodgepole pine in the stand; however, because lodgepole is a small component of the stand, successional implications of mountain pine beetle killing lodgepole are not likely to be large. The remaining 9 habitat type/cover type/structure class combinations contained low mountain pine beetle APIs. The APIs were not as informative in this sample due to small sample sizes within each HT/FT/SC combination. As more Bailey's ecosections are analyzed and sample sizes grow, the API data should become more useful.

Observed transitions in forest types with lodgepole pine, 1935 to 1975 eras in M332a

In the 26 HT/FT/SC combinations occurring in the 1935-era sample, the most frequent successional role of lodgepole pine was dominant seral. From the 26 HT/FT/SC combinations with the potential for mountain pine beetle activity in lodgepole occurring in the 1935 era sample, a total of 75 forest type/structure class transitions occurred from the 1935 era to the 1975 era. Of these 75 transitions, 65 follow the pattern described by stands impacted by the mountain pine beetle; i.e., succession was accelerated and/or structure class was altered. Ten transitions had outcomes which were not obviously influenced by mountain pine beetle activity. In these 10 transitions, either the mountain pine beetle was not active or its impact was overshadowed by other disturbance factors (Table 6.41).

Table 6.41: Transitions in M332a with the potential for mountain pine beetle activity.

# Transitions	Impact on Cover Type	Impact on Structure Class	Notes on Transitions
5	Push to climax	Stalled	MPB activity may help push to climax forest type
20	Push to climax	Prevent closure	MPB activity may help push to climax forest type
14	Push to climax	early-seral	MPB activity may help push to climax forest type
2	Push to climax	Maintain same structure class	MPB activity may help push to climax forest type
5	Push to climax	Increase density	MPB activity may help push to climax forest type

15	Push to climax	Normal	MBP activity may help push to climax forest type in all but 3/DFGFLP/2 to GFLP/3 where no beetle activity evident
3	Maintain seral	Stalled	MPB activity not evident
5	Maintain seral	Prevent closure	MPB activity consistent with observed structure class change for 3 of 5; no MPB activity evident for 2/DFLP/4 to DFLP/4 or 7/AFLPS/2 to LP4
2	Maintain seral	early-seral	MPB activity consistent with observed forest type and/or structure class change
2	Maintain seral	Maintain same structure class	MPB activity not evident
2	Maintain seral	Normal	MPB activity not evident
1	No change	Prevent closure	MPB may have impacted structure class

For the 65 transitions that were consistent with mountain pine beetle activity, the majority (59) had forest type conversions to more shade-tolerant species. In many cases, lodgepole pine went from being a major stand component (i.e., being part of the forest type designation) to being a minor component (not part of the forest type designation). Lodgepole pine was most frequently replaced by Douglas-fir, grand fir, subalpine fir, and cedar.

For two transitions (2/DFLP/4 to DFPP/4 and 2/LP/4 to nonforested), there was not a shift from seral to more shade-tolerant species; however, lodgepole was removed as a significant stand component (no longer part of the forest type designation). In 2 transitions lodgepole pine was not a significant enough component of the stand to be incorporated in the forest type designation. In these 2 transitions, the forest types and structure classes (9/DF/4 to DF/4 and 3/GF/4 to GF/4) were the same in the 1935-era sample and the 1975-era sample. Since the structure class was a 4, and both combinations had high or moderate calculated API values for mountain pine beetle in lodgepole pine, it is possible that the mountain pine beetle was active in these stands, removing lodgepole from the over story and preventing closure. It is more likely, however, that root disease (which had a moderate rating in these combinations) played a larger role in preventing closure. In one transition (2/DFLP/2 to DFLP/4) the structure class changed from a closed pole-sized stand to a mature stand with openings, consistent with mountain pine beetle activity which prevents closure and moves stands to an earlier structure class by removing susceptible lodgepole pine trees.

Conclusions for M332a based on forest type analysis

From data gathered in the broad scale analysis, major changes in the size, composition, and nature of the lodgepole pine forests in M332a are evident from the 1935-era and the 1975-

era samples. Data calculated in the form of mountain pine beetle action probability indices from the 1975-era sample and applied to the 1935-era HT/FT/SC combinations show that the mountain pine beetle may have played a significant role in some of the changes observed in the lodgepole pine forests. Also, observed transitions in these forests are consistent with what would have been predicted had the mountain pine beetle been active.

In the 1935-era data, there were relatively equal amounts of pure lodgepole pine forest types (734 hectares or 52 percent) and mixed conifer stands with a significant lodgepole component (688 hectares or 48 percent). By the the 1975 era, however, the total number of hectares with a significant lodgepole pine component had decreased from 1422 hectares to 1056 hectares (a reduction of 25 percent) and the amount of pure lodgepole pine forest type had shrunk to 215 hectares (a reduction of 61 percent). In the 1975-era sample, pure lodgepole pine forest types constituted only 20 percent of the forest types with lodgepole as a major stand component (or 215 hectares out of 1056 hectares with lodgepole as a major component). This change in the proportion of lodgepole is consistent with mountain pine beetle activity and a reduction in fire impacts.

In the 1935-era data, the pure lodgepole pine forest type forests were fairly evenly distributed between structure classes 1 (seedling/sapling), 2 (poles), and 4 (mature, canopy opening up). From the 1935 era to the 1975 era, the beginning structure class seemed to impact the ending forest type. For example, of the hectares with pure lodgepole pine forest types in structure class 1 in the 1935 era, 60 percent remained in a pure lodgepole pine forest type in the 1975 era; whereas, in structure class 2 in the 1935 era, only 19 percent remained in pure lodgepole pine forest types and 75 percent converted to mixed conifer forest types with a significant lodgepole pine component. In structure class 4, only 1 percent of the hectares remained in pure lodgepole pine forest type by the 1975 era, and 44 percent of the hectares converted to a forest type with no significant lodgepole pine component.

Data from the 1975-era sample indicates that, on all of the sites which supported lodgepole pine forest types, lodgepole pine played a minor or dominant seral role. In the early structure classes, trees are often too small to support large populations of mountain pine beetles, and lodgepole pine still has the advantage over more shade-tolerant species by virtue of its rapid growth; therefore, seedling/sapling stands would not be expected to change to another forest type. In the 40 years between samples some of these stands undoubtedly became susceptible to beetles and, following attack, species composition changed to more shade-tolerant species. However, the majority of the stands which had been seedlings/saplings in the 1935 era, remained in a pure lodgepole forest type in the 1975 era. In structure class 2 (pole sized), more of the stands are capable of supporting mountain pine beetle infestations so the larger proportion of these stands in our sample that moved from a pure lodgepole forest type to a mixed conifer with significant lodgepole component and mixed conifer without a significant lodgepole component is also consistent with the successional roles described for mountain pine beetle. The mountain pine beetle is capable of moving pure lodgepole stands to mixed conifer stands with and without significant lodgepole pine components in a relatively short period of time.

The structure class 4 pure lodgepole forest type conversion data rounds out the successional story presented above. In structure class 4, stands are mature and breaking up. Considering that there were no major fires in our sample during the 40 years between sample dates, it is logical that the lodgepole pine in mature forests would mostly drop out as a major stand component. The mountain pine beetle may have accelerated this process.

A change in the amount of fire is also likely to influence both the frequency of mountain pine beetle-mediated successional changes and the amount of forests susceptible to significant mountain pine beetle impacts. The total number of hectares in pure lodgepole pine forest types diminished significantly from the 1935 era to the 1975 era. In addition, the amount of pure lodgepole pine generated from other, non-lodgepole cover types was small (only 525 hectares). Of the pure lodgepole pine forest type generated, 421 hectares originated in areas considered nonforested and the remaining hectares had been white pine or larch/Douglas-fir cover types. Most of the nonforested areas were classified as recent burns in the 1935-era survey. In the future, without hot fires, it is unlikely that significant amounts of pure lodgepole pine forest types will be created. It is in pure lodgepole pine forests that mountain pine beetles have their most dramatic effects, causing rapid changes in forest types and structure classes in short periods of time.

Approximately 2,087 hectares of mixed forests with a significant lodgepole pine component existed in the 1975-era sample on hectares occupied in the 1935-era sample by forests that were not classified as lodgepole pine cover type. Approximately 41 percent of these mixed lodgepole pine forests grew on sites that had been recently burned in the 1935 era, and 38 percent grew on sites which had been mixed conifer. For lodgepole pine to increase in abundance on sites dominated by other, more shade tolerant, species is inconsistent with vegetational succession, so other disturbance factors, such as root disease, must have been present to aid in the increase of lodgepole pine. Fires would also have been likely causes for the increase in lodgepole pine, but none were recorded in our sample between the 1935 era and the 1975 era.

As lodgepole pine increases in abundance on the landscape, so does the potential role for mountain pine beetle in causing successional change. With the emphasis on fire suppression, lodgepole pine in the future will likely be a less dominant component of stands. In mixed-conifer stands, lodgepole pine abundance will more likely be determined by the amount of mixed severity fires and other insect and disease disturbances which give lodgepole pine a competitive advantage over the other species. Because lodgepole pine will only be one of many species in a stand, mountain pine beetle will likely serve to thin the lodgepole pine component from above in these stands, and the "outbreaks" of mountain pine beetle that removed most, if not all, of the lodgepole pine component in a short period of time will not develop. In these mixed-conifer stands, mountain pine beetle will impact stand composition by selectively removing the larger lodgepole pine, and affect stand structure by creating canopy openings. It may also impact fire frequency by creating light fuels that may help create areas appropriate for limited lodgepole pine regeneration, but it is unlikely that mountain pine beetle impacts alone in mixed-conifer stands will generate enough fuels to set the stage for catastrophic fires and subsequent regeneration to pure lodgepole pine.

Cover Type Analysis for Mountain Pine Beetle in Lodgepole Pine in M333d: API Analysis

In 1975-era data for M333D, there were 17 habitat type group/cover type/structure class (HT/CT/SC) combinations (polygon classes) that had calculated mountain pine beetle in lodgepole pine API values. These combinations occurred in habitat type groups 2, 3, 5, 7, 9, and 10 and with cover types (CT) 1, 5, 7, and 11. In HT/CT/SC combinations with the potential for mountain pine beetle activity in lodgepole pine occurring in the 1935-era data, lodgepole pine usually played a minor or dominant seral role.

Eleven of the 17 polygon classes were represented in the historic data. Five of these classes had a lodgepole pine cover type. For these five classes, the observed transitions were consistent with mountain pine beetle activity impacts upon succession, i.e., the cover type changed to one with less lodgepole and/or the structure class was stalled, moved to an earlier structure class (1 or 2), or was opened up (moved to a SC 4).

The transitions in the remaining six classes are more difficult to characterize in terms of mountain pine beetle impacts on succession because these polygon classes have cover type designations which do not give much information on how much lodgepole pine is present. The stand conditions on the hectares with high mountain pine beetle API values were highly conducive to mountain pine beetle. The beetle could have been actively removing the lodgepole pine present in the stands. This activity, however, would not result in a cover type change so would not result in a detectable successional change.

Observed transitions in lodgepole pine cover types (7) from the 1935 era to 1975 eras

There were 71 observed transitions in polygon classes that had a lodgepole pine cover type in the 1935 era. In the 1935 era, 1,612 hectares had a lodgepole pine cover type. In the 1975 era, only 911 hectares had a lodgepole pine cover type (Figure 6.45). All of the hectares in lodgepole pine cover types in the 1975 era were in lodgepole cover types in the 1935 era, i.e., no lodgepole cover types were recruited from another cover type.

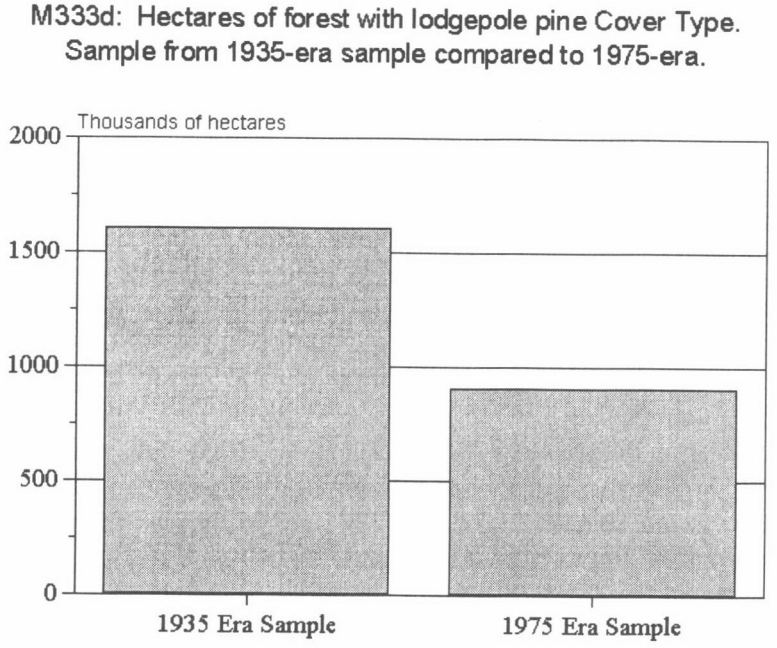

Figure 6.45: Hectares of forest with lodgepole pine cover type, 1935 era and 1975 era, M333d.

Of the 1,612 hectares of lodgepole pine in the 1935 era, 911 hectares stayed in lodgepole pine cover types (56 percent); 289 hectares transitioned to CT 11 (subalpine fir, mountain hemlock, whitebark pine) (18 percent); 179 hectares transitioned to CT 1 (western white pine) (11 percent); 135 hectares transitioned to CT 5 (Douglas-fir) (8 percent); 33 hectares transitioned to CT 3 (larch/Douglas-fir) (2 percent); and the remaining 65 hectares transitioned to non-forest

or ponderosa pine, western hemlock/grand fir, cedar/grand fir, grand fir, or Engelmann spruce cover types. (less than 1 percent) (Figure 6.46).

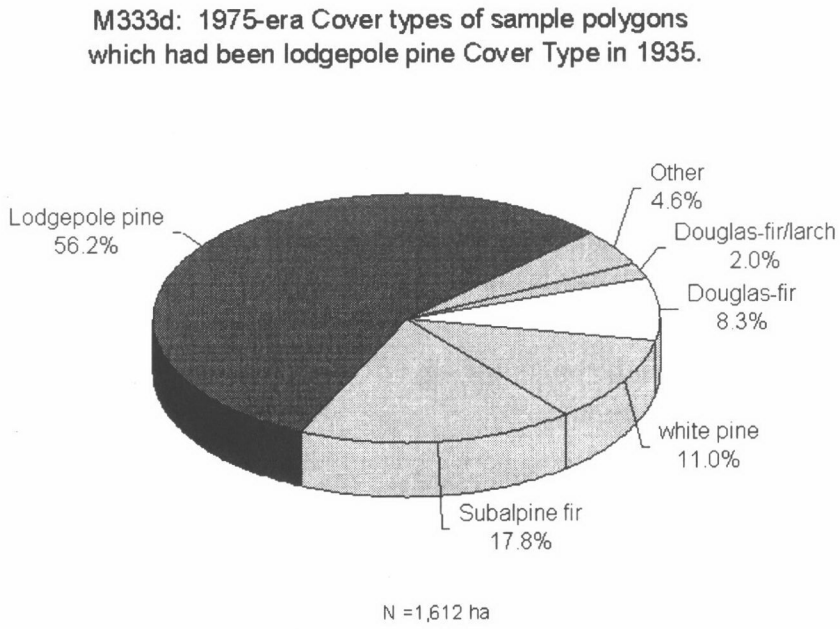

Figure 6.46: 1975 era cover types of sample polygons that had been lodgepole pine cover type in 1935 era, M333d.

There were dramatic changes in the structure class distribution of lodgepole pine cover types between the 1935 era and the 1975 era. In the 1935 era, approximately 63 percent (1,012 hectares) of lodgepole pine cover types were in structure class 1, 35 percent (564 hectares) were in structure class 2; and 2 percent (36 hectares) were in structure class 4. In the 1975 era, 81 percent of forests with lodgepole pine cover types were in structure class 2 (736 hectares); 15 percent (134 hectares) were in structure class 1; and 4 percent (41 hectares) were in structure class 4 (Figure 6.47).

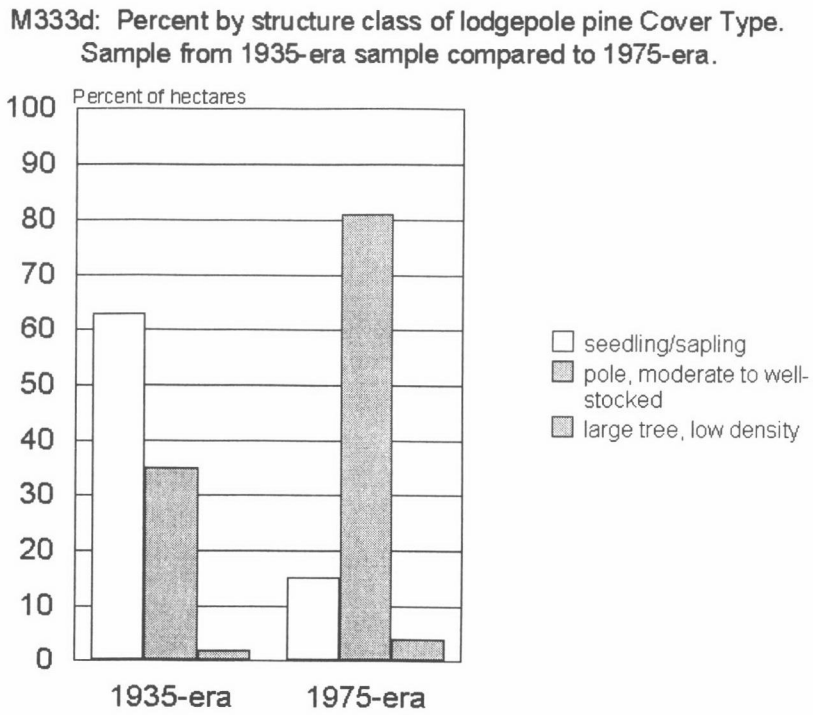

Figure 6.47: Percentage of hectares in structure class of lodgepole pine cover type, 1935 and 1975 eras, M333d.

Most of the transitions in lodgepole pine cover type in the 1935 era were consistent with mountain pine beetle activity (Table 6.42). In terms of area, 43 percent (701 hectares) of the lodgepole pine cover type in the 1935-era sample transitioned to a different cover type indicating that lodgepole pine abundance was reduced, potentially by mountain pine beetle activity. Eleven percent (172 hectares) of the sample stalled, e.g. succession did not move forward. This is consistent with mountain pine beetle activity removing larger diameter trees preventing stands from changing structure classes. In 7 percent (115 hectares) of the 1935-era lodgepole pine cover type hectares, structure class changes were consistent with mountain pine beetle activity removing larger trees thus creating openings or moving the structure class back.

The remaining 39 percent of the 1935-era lodgepole pine cover type hectares (624 hectares) experienced transitions which were contrary to what would be expected if mountain pine beetle was active. On these hectares either the mountain pine beetle was not active or its impacts were overshadowed by other disturbance factors.

Table 6.42: Transitions by cover type in M333d with the potential for mountain pine beetle lodgepole pine activity.

# Transitions	Successional Impact	Notes on Transition
50	Change in cover type	Mountain pine beetle activity may have resulted in the change from a lodgepole pine CT (LP > 50 percent) to another cover type with less lodgepole
6	Stalled: No successional change observed	Mountain pine beetle activity may have prevented succession from moving forward by removing larger lodgepole pine and preventing canopy closure.
5	No change in cover type but a change in structure class	In two of these transitions, structure class moved from a 4 to a 1 or 2. Mountain pine beetle may have facilitated this by removing the remaining larger diameter lodgepole pine resulting in a structure class shift. In one transition, structure class moved from a 2 to a 4. Mountain pine beetle may have facilitated this by creating openings in the canopy, preventing closure. In the remaining 2 transitions, structure class moved from a 2 to a 1. Mountain pine beetle may have removed all of the larger trees in these transitions.
10	Successional changes contrary to what would be expected if Mountain pine beetle was active	Either the Mountain pine beetle was not active in these transitions or its impacts were overshadowed by other factors, including other disturbance agents.

Conclusions for M333d based on cover type analysis

Cover type analysis indicated a 44 percent reduction in the number of hectares occupied by lodgepole pine cover types from the 1935 era to the 1975 era (Figure 6.45). The cover type analysis also indicated that lodgepole pine cover types were not recruited from other forest types. There was also a significant shift in the structure class composition of lodgepole pine forest types from the 1935 era to the 1975 era (Figure 6.47). In the 1935 era, most of the area in lodgepole pine cover types were in structure class 1 (63 percent or 1012 hectares) or 2 (35 percent or 564 hectares), with the remaining 2 percent (36 hectares) in structure class 4. By the 1975 era, the proportion of lodgepole pine cover types in structure class 2 had increased to 81 percent (736 hectares), 15 percent (134 hectares) were in structure class 1, and 4 percent (41 hectares) in structure class 4. The changes in amount of lodgepole pine cover type and relative proportion of structure classes are likely the result of lack of fire and mountain pine beetle activity between the 1935 era and the 1975 era.

It is evident that there has been a decrease in the amount of lodgepole pine cover types, and stands with greater than 50 percent lodgepole pine are more susceptible to mountain pine

beetle successional impacts. The structure class changes observed between the 1935 era and the 1975 era indicate that on the hectares of lodgepole pine cover type remaining, there is less diversity in structure so there is a higher likelihood that the majority of lodgepole cover types will become susceptible to mountain pine beetle at the same time. Stands in structure class 3 are the most prone to mountain pine beetle activity, though susceptibility may begin in the later portion of structure class 2. In the 1975 era, 81 percent of the remaining lodgepole pine cover types were in a structure class 2.

Forest Type Analysis for Mountain Pine Beetle in Lodgepole Pine in M333d

API analysis

Action probability index (API) data could be calculated for 19 of the 26 HT/FT/SC combinations occurring in the 1935-era data. Eleven of the 19 combinations contained high or moderate mountain pine beetle APIs, even though two combinations did not have lodgepole pine in the forest type definition (i.e., lodgepole pine did not comprise more than 30 percent of the canopy cover). A high API value for a non-lodgepole pine forest type indicates that there are susceptible lodgepole pine in the stand; however, since lodgepole is a small component of the stand, successional implications of mountain pine beetle killing lodgepole are not likely to be large. The remaining 8 HT/FT/SC combinations contained low mountain pine beetle APIs. The APIs were not as informative in this sample due to small sample sizes within each HT/FT/SC combination. As more Bailey's ecosections are analyzed, and sample sizes grow, the API data should become more useful.

Observed transitions in forest types with lodgepole pine, 1935 to 1975 eras

In the 26 HT/FT/SC combinations with the potential for mountain pine beetle activity in lodgepole pine occurring in the 1935-era data, lodgepole pine usually played a minor or dominant seral role. From these 26 HT/FT/SC combinations, a total of 65 forest type/structure class transitions occurred from the 1935 era to the 1975 era. Forty-eight of these transitions follow the pattern described by stands impacted by mountain pine beetle activity: i.e., succession was accelerated and/or structure class was altered. Fifteen transitions had outcomes that were not obviously influenced by mountain pine beetle activity, and two transitions had outcomes contrary to what would be expected if mountain pine beetle was playing a successional role. In these last 17 transitions, either the mountain pine beetle was not active or its impact was overshadowed by other disturbance factors (Table 6.43).

Table 6.43: Transitions in M333d with the potential for mountain pine beetle activity.

# Transitions	Impact on Forest Type	Impact on Structure Class	Notes on Transitions
4	Push to climax	Younger/smaller	MPB activity may help push to climax forest type
11	Push to climax	Stalled in young/small	MPB activity may help push to climax forest type in all but 2/DFL/2 to DF/2 where no apparent MPB influence
6	Push to climax	Prevent closure	MPB activity may help push to climax forest type in all but 2/DFL/2 to DF/4 where MPB activity may open canopy
8	Push to climax	None: becomes larger/denser	MPB activity may help push to climax forest type
5	Push to climax	Maintain same structure class	MPB activity may help push to climax forest type in 2; no apparent MPB affects in 9/DFL LP/2 to AFDFLP/2; 9/DFL LP/2 to AFLPMH/2; or 9/DFL LP/2 to DFGFLP/2
1	Push to climax	Increase density	MPB activity may help push to climax forest type
9	Maintain early seral	Younger/smaller	MPB activity may help push structure class; MPB in conjunction w/ other agents in 9/DFLPPP/4 to LP/2; no apparent MPB affects in 2/DFL/2 to DFPP/1
2	Maintain early seral	Stalled in young/small	MPB activity not evident
3	Maintain early seral	Prevent closure	MPB activity may help push structure class
5	Maintain early seral	Maintain same structure class	MPB activity may help change forest type in one transition; MPB activity not evident in other 4
5	Maintain early seral	None: becomes larger/denser	MPB activity may help push to climax forest type in 3 transitions, MPB activity not evident in other 2

2	Initiate early seral	Younger/smaller	MPB activity may help change FT in one transition and structure class in another
2	Initiate early seral	Prevent closure	MPB activity not evident in 2/DFL/2 to PP/4, and opposite of what would be anticipated in 2/DFL/2 to LP/4
1	Initiate early seral	Maintain Same structure class	MPB activity would produce opposite of 9/AFL LP/4 to LP/4
1	No change	None: becomes larger/denser	MPB activity not evident

For the 48 transitions that were consistent with mountain pine beetle activity, the majority (35) had forest type conversions, mostly to more shade tolerant species. Most of the forest type changes were in the form of lodgepole pine being identified as a component of the forest type in the 1935 era but not in the 1975 era. In the remaining 13 transitions, structure classes either moved from a 2 to a 4, a 3 to a 4, or a 4 to a 2. The beetles reduce the amount of lodgepole in the stand, remove the larger lodgepole and leaving younger trees causing the stand to move to an earlier structure class, and create openings which prevent canopy closure.

Conclusions based on forest type analysis of M333d

From data gathered in the broad scale analysis major changes in the size, composition, and nature of the lodgepole pine forests in M333d are evident from the 1935-eras and the 1975-era samples. Data calculated in the form of mountain pine beetle action probability indices from the 1975-era sample and applied to the 1935-era habitat type group/forest type/structure class combinations show that the mountain pine beetle may have played a significant role in some of the changes observed in the lodgepole pine forests, and the observed transitions in these forests are consistent with what would have been predicted had the mountain pine beetle been active.

In the 1935-era sample, there were relatively equal amounts of pure lodgepole pine forest types (969 hectares or 48 percent) and mixed conifer stands with a significant lodgepole component (1,042 hectares or 52 percent). By the 1975 era, the total number of hectares with a significant lodgepole pine component had increased from 2,011 hectares to 3,962 hectares (a 97 percent increase) and the amount of pure lodgepole pine forest type had increased to 1,089 hectares (a 12 percent increase) (Figure 6.48). In the 1975-era sample, pure lodgepole pine forest types constituted 27 percent of the forest types with lodgepole as a major stand component (or 10,89 hectares out of 3,962 hectares with lodgepole as a major component). This change in the proportion of pure lodgepole forest types to mixed lodgepole forest types is consistent with mountain pine beetle activity and a reduction in fire impacts.

In the 1935-era data, the pure lodgepole pine forest type forests were mostly in structure class 1 (seedling/sapling), with a significant amount in structural stag 2 (poles), and a minor amount in structure class 4 (mature, canopy opening up) (Fig 6.49). The large proportion of pure lodgepole pine forests in structure class 1 is likely due to the impacts of the 1910 fires that swept through M333d and regenerated a large portion of the area. By the 1975 era, only 43 percent of the pure lodgepole pine forest type remained; 40 percent had converted to a mixed conifer with

significant lodgepole component; and 15 percent had converted to a forest type without lodgepole pine as a dominant component (Figure 6.50). Data from the 1975 era indicates that on all of the sites that supported lodgepole pine forest types, lodgepole pine played a minor or dominant seral role. In the early structure classes, trees are often too small to support large populations of mountain pine beetles, and lodgepole pine still has the advantage over more shade-tolerant species by virtue of its rapid growth: therefore the early structure classes would not be expected to lose their lodgepole pine component in the 40 years between samples. The fact that such a large proportion of the pure lodgepole pine forest types converted to a mixed conifer with a significant lodgepole pine component does indicate, however, that mountain pine beetle may have been active helping to accelerate succession.

The total number of hectares in pure lodgepole pine forest types remained fairly constant from 1935 to 1975 eras. This fact is somewhat surprising since in the Rocky Mountains most pure lodgepole pine forests are created as a result of hot fires and there were no fires in the sample during the 40 year sample horizon, and approximately 56 percent of the forests that were pure lodgepole pine forest types in the 1935-era sample transitioned into something else.

Of the hectares that converted to pure lodgepole pine forest types during the 40-year period between samples, 80 percent (421 hectares) were classified as non-forested in the 1935 era (Figure 6.51). A large proportion of these hectares were most likely brush fields that were created in the 1910 fires and had not regenerated sufficiently by the 1935 era to be considered forested. Approximately 10 percent (51 hectares) were in seedling/sapling white pine stands in the 1935 era. On these hectares, the impact of the white pine blister rust, an introduced pathogen which kills white pine- most significantly young white pine, favored the development of lodgepole pine over white pine. The remaining hectares which became pure lodgepole pine forest types in the 1975 era started out as Douglas-fir/ larch and larch forest types in the 1935 era. Conversion of these stands to lodgepole pine is contrary to what would be expected if succession was responsible, therefore some disturbance agent, possibly another insect or pathogen, is involved. Without hot fires, and since the majority of the white pine forest types have been converted to other forest types, it is unlikely that significant amounts of pure lodgepole pine forest types will be created into the future, and it is in pure lodgepole pine forests that mountain pine beetles have their most dramatic impacts, causing rapid changes in forest types and structural stages in short periods of time.

Lodgepole pine increased in abundance from the 1935-era sample on approximately 2087 hectares of forests so that it became part of the forest type designation in the 1975-era sample. Approximately 38 percent of these mixed lodgepole pine forests grew on sites which were mixed conifer without significant lodgepole pine components in 1935-era sample, 16 percent grew on sites that were in white pine forest types, and an additional 5 percent grew on sites with other single species forest types (Figure 6.52). For lodgepole pine to increase in abundance on sites dominated by other species is inconsistent with vegetational succession, so other disturbance factors, such as white pine blister rust, or root disease, must have been present to aid in the increase of lodgepole pine.

As lodgepole pine increases in abundance on the landscape, so does the potential for mountain pine beetle activity to cause successional impacts. With continued emphasis on fire suppression, lodgepole pine is unlikely to occur in pure stands. In mixed conifer stands, lodgepole pine abundance will more likely be determined by the amount of mixed severity fire and other insect and disease disturbances that give lodgepole pine a competitive advantage over the other species. Because lodgepole pine will only be one of many species in a stand, mountain

pine beetle will likely serve to thin the lodgepole pine component from above in these stands, and the "outbreaks" of mountain pine beetle that removed most, if not all, of the lodgepole pine component in a short period of time will not develop. In these mixed-conifer stands, mountain pine beetle will impact stand composition by selectively removing the larger lodgepole and stand structure by creating canopy openings. It may also impact fire frequency by creating light fuels that may help create areas appropriate for lodgepole pine regeneration, but it is unlikely that mountain pine beetle impacts alone in mixed conifer stands will generate enough fuels to set the stage for catastrophic fires and regeneration to pure lodgepole pine.

MOUNTAIN PINE BEETLE AND WESTERN PINE BEETLE SUCCESSION FUNCTIONS IN PONDEROSA PINE

By Carol Bell Randall

The mountain pine beetle, *Dendroctonus ponderosae* Hopk., and western pine beetle, *Dentroctonus brevicomis*, are the two most destructive bark beetles that attack ponderosa pine in the United States. Successful beetle attacks kill the host.

The mountain pine beetle typically kills groups of ponderosa pines, often on a large scale, both in mature and in young overstocked stands. Mostly, this beetle is a primary tree killer, but at times it occurs as secondary; for example, in association with the western pine beetle (Furniss and Carolin 1977). Mountain pine beetle outbreaks are most devastating in stands that are pure or nearly pure ponderosa pine, are essentially even-aged, are 50-100 years old, have average DBHs between 8 and 12 inches, and have a stem basal area generally in excess of 150 square feet/acre (Sartwell and Stevens 1975).

The western pine beetle devastated stands of large, overmature, decadent ponderosa pines in the first half of the 20th century. Where stands of this nature still exist, there is great potential for damage. Even single, large, old, slow-growing or diseased ponderosa pines are very susceptible to attack. Recently, this beetle has become especially aggressive in second growth stands, killing trees 6 inches or larger in diameter, including apparently healthy trees. Trees are characteristically killed in groups, primarily in dense, overstocked stands of pure, even-aged pines. Drought-weakened trees are especially susceptible, and outbreak populations can build to very high levels under these conditions (Livingston 1991).

Succession Functions of the Mountain Pine Beetle and Western Pine Beetle as Related to the Successional Role of Ponderosa Pine

The impact that mountain pine beetle and western pine beetle attacks on ponderosa pine will have on stand succession depends upon the successional role that ponderosa pine plays in a stand. Ponderosa pine occupies a climax role towards the severe limits of its environmental range, and becomes increasingly seral with increasingly favorable environment (Oliver and Ryker 1990). On more favorable sites, the pine encounters severe competition with other tree species and must establish opportunistically when disturbance reduces competition and creates a seed-bed. On these sites, ponderosa pine is usually seral to Douglas-fir and true firs, or, in North Idaho and Western Montana, Engelmann spruce and occasionally subalpine fir.

There are three commonly recognized successional roles for ponderosa pine: minor seral, dominant seral, and climax (Steele 1988). Mountain pine beetle and western pine beetle may be found killing ponderosa pine in any of these roles. The beetles' impact on ponderosa pine does not usually result in an alteration of stand succession unless ponderosa pine is a major stand component (Figure 6.48).

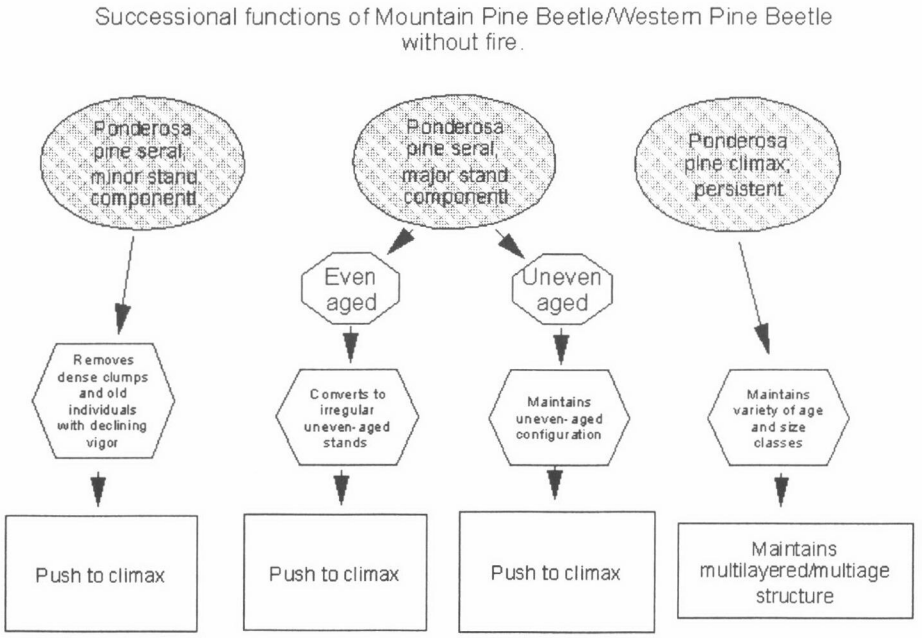
Successional functions of Mountain Pine Beetle/Western Pine Beetle without fire.
Ponderosa pine seral, minor stand component
Ponderosa pine seral, major stand component
Ponderosa pine climax; persistent
Even aged
Uneven aged
Removes dense clumps and old individuals with declining vigor
Converts to irregular uneven-aged stands
Maintains uneven-aged configuration
Maintains variety of age and size classes
Push to climax
Push to climax
Push to climax
Maintains multilayered/multiage structure

Figure 6.48: Succession functions of mountain pine beetle/western pine beetle without fire.

Ponderosa pine as minor seral

Where ponderosa pine is a minor seral component of the stand, the succession function of the mountain pine beetle and western pine beetle is to accelerate succession by removing mature ponderosa pine from the stand and favoring the dominance of more shade-tolerant, climax species. Ponderosa pine is considered a minor seral species where it has historically occurred in relatively small numbers and was never more than a minor component of the stand. On these minor seral sites, ponderosa pine has little opportunity to dominate the site at any seral stage. In many of these stands, ponderosa pine is such a minor component that the impact of the beetles removing seral ponderosa pine may not have a major impact on the composition or structure of the stand. The larger the ponderosa pine component in the stand, the more impact the beetles may have.

In many of these habitat types, forest managers tried to establish ponderosa pine in plantations. Initially, these plantations did well, but eventually the plantations tended to fail due to intense shrub competition, repeated snow damage, and/or root disease. Most of the plantations failed before the ponderosa pine reached a size and age class conducive to bark beetle attack; however, it is possible that beetles may have caused conversions in some plantations.

Ponderosa pine is often a minor seral on habitat types in the western redcedar series. It is also considered a minor seral on some habitat types in the Douglas-fir and grand fir series.

Ponderosa pine as a dominant seral

Where ponderosa pine is a dominant seral component of the stand, the succession function of mountain pine beetle and western pine beetle is also to accelerate succession. Ponderosa pine can dominate the site at some seral stage: much of the original ponderosa pine forests fell

into this category. Ponderosa pine tends to grow best on these sites, historically due to frequent, low-intensity surface fires that killed competing conifer species and prepared a seed-bed for the pine. Timber harvesting and lack of fire have combined with succession to reduce the number of acres of ponderosa pine forests on these sites. Outbreaks of bark beetles may dramatically alter both stand species composition and structural stage. By removing the larger, dominant ponderosa pine the beetles favor the development of more climax communities of Douglas-fir, grand fir, or Engelmann spruce. In the short term beetle activity decreases the density of the stands, prevents canopy closure, and maintains smaller trees. In the longer term, beetle activity may actually increase the density of stand by enabling the development of large number of shade tolerant species which out compete seral ponderosa pine by shading it out.

Ponderosa pine is a dominant seral on many habitat types in the grand fir, and Douglas-fir series.

Ponderosa pine as climax

In these stands the mountain pine beetle and western pine beetle do not affect species composition as much as structural stage. Sites where ponderosa pine is climax typically occur within the lower forest ecosection where it grades into non forest communities. In stands where ponderosa pine is the climax species, mountain pine beetle activity tends to convert even age stands to irregular, uneven age stands and maintains stands in uneven aged configurations by consistently killing mid-range diameter (7.1- to 13-inch) trees (Lessard 1981). The mountain pine beetle does not seem to have a large impact on ponderosa pines outside of this diameter class range. The western pine beetle also converts even age stands to irregular, uneven age stands by removing the larger trees and creating openings which promote the establishment of ponderosa pine seedlings.

Ponderosa pine is the climax species on the ponderosa pine series.

Mountain Pine Beetle and Western Pine Beetle, Fire, and Succession

Fire plays many important succession roles in ponderosa pine stands (Crane and Fischer 1986). On the driest sites, fire maintains grasslands by precluding tree regeneration through frequent burning; maintains open stands by reducing the number of seedlings, removing dense under stories of saplings or pole sized trees, or thinning over story trees; or encourages tree regeneration by exposing mineral soil and removing competing vegetation. On more favorable sites, relatively frequent fires have been important in establishing and maintaining open, old growth ponderosa pine stands by preparing seedbeds for ponderosa pine regeneration; controlling stocking levels in young stands; thinning suppressed pole sized stands; maintaining a ponderosa pine "fire climax" on Douglas-fir habitat types by killing the Douglas-fir under story; maintaining open park like stands of ponderosa pine or ponderosa pine/Douglas-fir; preventing the development of fuel ladders of saplings or small poles that could carry fire into the crowns of mature stands; and pruning back mistletoe infected branches in the lower crowns, thus limiting the mistletoe plants to a sometimes inconspicuous presence high in the forest canopy. Frequent fires controlled stand density and stand structure, which in turn determined a stand's susceptibility to beetle activity.

The last 100 years have produced unplanned, radical changes in stand structure, fuel loadings, and the role of fire in ponderosa pine ecosystems (Arno 1988). The succession changes are a result of the cessation of frequent burning linked to 1) initiation of heavy livestock grazing in the 1800s which removed herbaceous fuels; 2) relocation of Native Americans to

reservations, which removed a source of ignitions; 3) the breakup of fuel continuity through European-American settlement and land use practices; and 4) the development of organized fire suppression (Pyne 1982; Lotan et al. 1985; Arno and Gruell 1986). With the cessation of frequent fires, the trend towards dense stocking and domination by shade-tolerant species favors other mortality factors such as bark beetles, dwarf mistletoe, and commandra blister rust in dense ponderosa pine; western spruce budworm, tussock moth, and root diseases in "firs"; Indian paint fungus in grand fir; and dwarf mistletoe in Douglas-fir (Fellin 1979; Mitchell and Martin 1980; Williams et al. 1980; McCune 1983; Carlson et al. 1983; Byler 1984).

Western Pine beetle traditionally was considered only a pest of large, decadent ponderosa pine. Pine stands that approached maturity were thinned by western pine beetle epidemics, and new trees grew up to replace those that were killed. Frequent fires maintained these ponderosa pine stands in an open, and vigorous condition until they reached maturity, so western pine beetle did not become a problem in younger stands. Likewise, mountain pine beetle outbreaks rarely developed in stands with fire maintained low stocking levels. With the reduction in fire, more ponderosa pine stands are becoming susceptible to bark beetle activity at a younger age. Fire is no longer thinning stands with the regularity it did in the past, and many more stands are reaching densities conducive to bark beetle outbreaks. Even the western pine beetle, once considered only a pest of old growth ponderosa pine, is taking advantage of the abundance of overstocked, second growth ponderosa pine.

Because of the reduction of fire, bark beetles are beginning to assume some of the functions fire traditionally occupied. Bark beetle activity is thinning second growth stands, but in a different way than fire. Bark beetle activity thins in patches, removing most susceptible individuals in a group. Frequent, low-intensity fire thinned trees more uniformly throughout a stand. Beetle activity only impacts ponderosa pine: other species, such as the true firs or Douglas-fir are not impacted and are actually favored to succeed pine as the dominant species. Fire kills other species, favoring ponderosa pine on the site. Bark beetle activity does nothing to reduce seedling/sapling levels or the amount of shrubs; frequent low-intensity fires would keep this type of vegetation at low levels. As a result, frequent, low-intensity fires reduced the likelihood of stand-replacing catastrophic fires, whereas bark beetle activity seems to favor them (Figure 6.49).

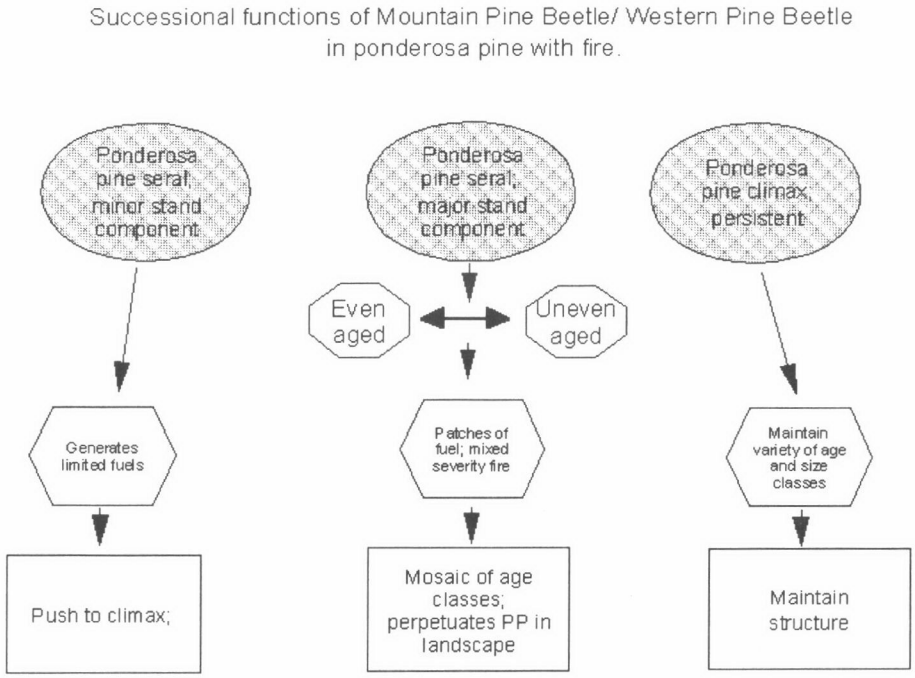
Successional functions of Mountain Pine Beetle/ Western Pine Beetle
in ponderosa pine with fire.
Ponderosa pine seral, minor stand component
Ponderosa pine seral, major stand component
Ponderosa pine climax, persistent
Even aged
Uneven aged
Generates limited fuels
Patches of fuel; mixed severity fire
Maintain variety of age and size classes
Push to climax;
Mosaic of age classes; perpetuates PP in landscape
Maintain structure

Figure 6.49: Succession functions of mountain pine beetle/western pine beetle in ponderosa pine with fire.

Cover Type Analysis for Mountain Pine Beetle and Western Pine Beetle in Ponderosa Pine in M332a

API analysis

In M332a, 1975-era data, there were eight habitat type group/cover type/structure class (HT/CT/SS) combinations (polygon classes), which had calculated bark beetle in ponderosa pine API values. These combinations occurred in habitat type groups 1, 2, 3, and 4, and cover types (CTs) 2, 2.8, and 5.

Only two of the eight polygon classes were represented in the 1935-era data. One class had a cover type of 2.8 and the other had cover type 5. For the class with a 2.8 cover type, all observed transitions were consistent with mountain pine beetle activity impacts upon succession: i.e., the cover type changed to one with less ponderosa pine and/or the structure class was stalled, moved to an earlier structure class (1 or 2), or was opened up (moved to a SS 4).

The polygons classified as cover type 5, by definition, have less than 25 percent of the stand boardfoot volume in ponderosa pine, but all of the hectares in the class HT 1/CT5/SC 2 received mountain pine beetle/western pine beetle API ratings. They would not have been rated for bark beetles unless they had at least 25 percent of the basal area in ponderosa pine. This probably means that the stands were borderline ponderosa pine cover types. All of the hectares in this class moved from a structure class of 2 to a structure class of 4. Pine bark beetles could have been actively removing the ponderosa pine from the stands, creating openings and resulting in the structure class shift from a 2 to a 4.

Observed transitions in ponderosa pine cover types from 1935 to 1975 eras

There were 26 observed transitions in polygon classes that had ponderosa pine cover types (2 or 2.8) in the 1935 era. In the 1935 era, 444 hectares had ponderosa pine cover types. Of these, 32 percent were in cover type 2.8, mostly pure ponderosa pine forests, and 68 percent were in cover type 2, relatively mixed ponderosa pine forest types. In the 1975 era, only 276 hectares had ponderosa pine cover types. Of these, 24 percent were in cover type 2.8, relatively pure ponderosa pine forests, and 210 hectares (76 percent) were in cover type 2, mixed ponderosa pine forest types. All of the hectares in ponderosa pine cover types in the 1975 era were in ponderosa pine cover types in the 1935 era, e.g., no ponderosa pine cover types were recruited from other cover types. Sixty four hectares of ponderosa pine cover type transitioned from cover type (CT) 2.8 in the 1935 era to CT 2 in the 1975 era.

Of the 444 hectares of ponderosa pine in the 1935 era, 62 percent stayed in ponderosa pine cover types; 26 percent transitioned to Douglas-fir cover type ; 5 percent transitioned to CT 11 (subalpine fir, mountain hemlock, or whitebark pine); 6 percent to grand fir or grand fir/cedar; and about 19 hectares became non-forested (Figure 6.50).

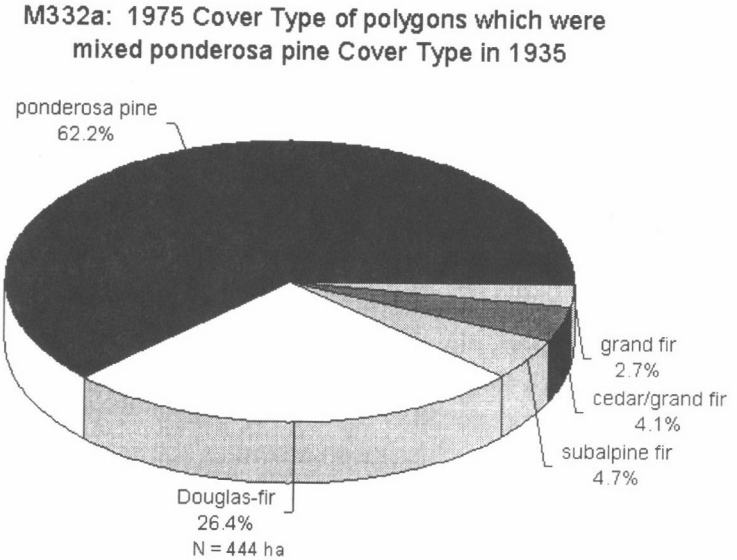

Figure 6.50: 1975-era cover types of polygons that had been mixed ponderosa pine cover type in the 1935 era, M332a.

There were minor changes in the structure class distribution between ponderosa pine cover types from 1935 to 1975 eras. In the 1935 era, approximately 56 percent of ponderosa pine cover types were in structure class 4, 32 percent were in structure class 3; and 12 percent were in structure class 2. In the 1975 era, 50 percent of forests with ponderosa pine cover types were in structure class 4; 14 percent were in structure class 3; 13 percent were in structure class 2; and 23 percent were in structure class 1 (Figure 6.51). The biggest change is the increase in the proportion of ponderosa pine cover types in structure class 1 (from 0 percent in the 1935 era to 23 percent in the 1975 era).

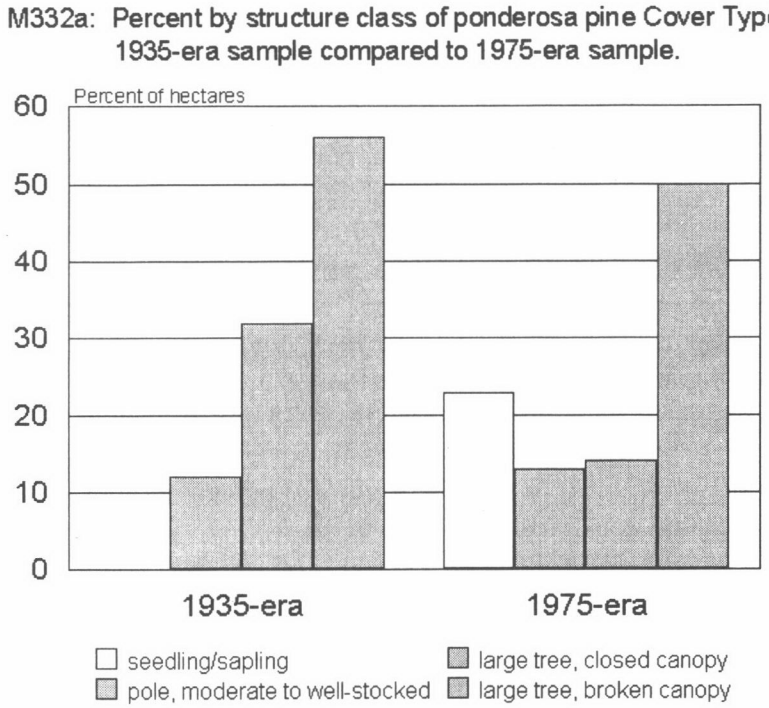

Figure 6.51: Percentages of structure class of ponderosa pine cover type, 1935 and 1975 eras, M332a.

Most of the transitions in ponderosa pine cover type in the 1935 era were consistent with mountain pine beetle or western pine beetle activity (Table 6.44). In terms of area, 52 percent the ponderosa pine cover type in the 1935-era sample transitioned to a different cover type, indicating that ponderosa pine abundance was reduced to below 25 percent of the stand (Figure 6.52), potentially by bark beetle activity. Thirteen percent of the sample (56 hectares) stalled; i.e., succession did not move forward. This is consistent with bark beetle activity removing larger-diameter trees and preventing stands from changing structure class. In 25 percent percent of the 1935-era ponderosa pine cover type hectares, structure class changes were consistent with bark beetle activity removing larger trees and thus creating openings or moving the structure class back.

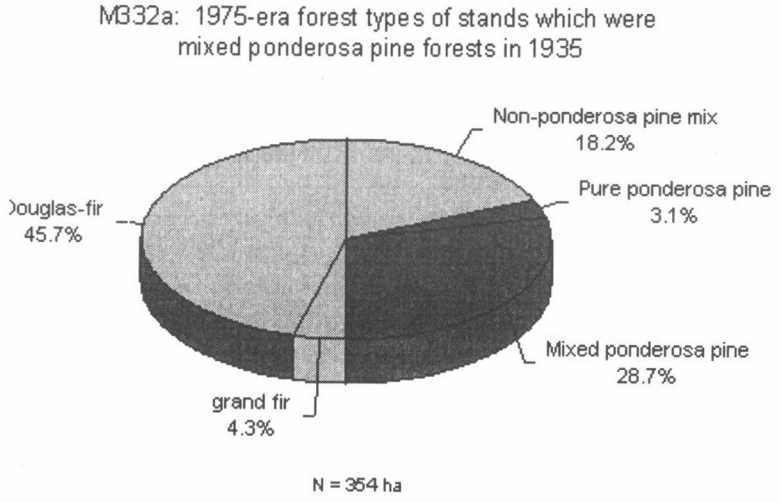

Figure 6.52: 1975-era forest types of stands that were mixed ponderosa pine forests in the 1935 era, M332a.

The remaining 10 percent of the 1935-era ponderosa pine cover type experienced transitions which were contrary to what would be expected if bark beetles were active. On these hectares, either beetles were not active or their impact was overshadowed by other disturbance factors.

Table 6.44: Cover type transitions in M332a with high probable influence from bark beetles in ponderosa pine.

# Transitions	Successional Impact	Notes on Transition
15	Change in cover type	Bark beetle activity may have resulted in the change from a ponderosa pine cover type to another cover type.
2	Succession suspended	Bark beetle activity may have prevented succession from moving forward by removing larger ponderosa pine and preventing canopy closure
6	No change in cover type but a change in Structure class	In one of these transitions, structure class moved from a 4 to a 1. Bark beetles may have facilitated this by removing the remaining larger-diameter PP, resulting in a structure class shift. In three transitions structure class moved from a 2 or 3 to a 4. Bark beetles may have facilitated this by creating openings in the canopy, preventing closure. In the remaining two transitions structure class moved from a 3 to a 2. Bark beetle activity may have facilitated this by removing the larger-diameter trees, leaving poles.
3	Successional changes contrary to what would be expected if mountain pine beetle was active	Either bark beetles were not active in these transitions or their impacts were overshadowed by other factors, such as succession or other disturbance agents

Conclusions for M332a based on cover type analysis

Cover type analysis indicated a 44 percent reduction in the number of hectares occupied by ponderosa pine cover types from 1935 to 1975 eras (Figure 6.53). Within these ponderosa pine cover types there was also a decrease in the amount of relatively pure ponderosa pine (CT 2.8) from 32 percent of ponderosa pine cover type in the 1935 era to 24 percent of ponderosa pine cover types in the 1975 era. The cover type analysis also indicated that ponderosa pine cover types were not recruited from other forest types, and that some of the pure ponderosa pine cover types in the 1935-era sample converted to more mixed ponderosa pine cover type in the 1975 era. The changes in amount of ponderosa pine cover type and relative proportion of pure and mixed ponderosa pine cover types are likely the result of lack of fire and bark beetle activity between the 1935 and 1975 eras. Ponderosa pine cover types, especially pure ponderosa pine cover types, are the most susceptible to bark beetle-influenced successional change.

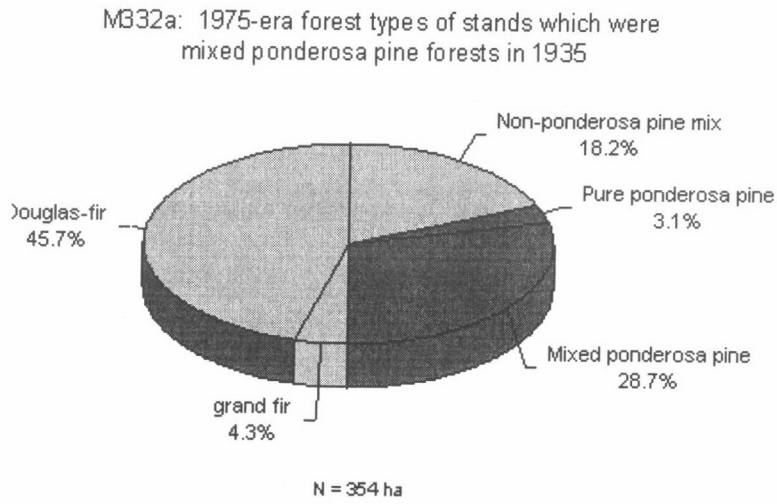

Figure 6.53: Hectares with a significant component of ponderosa pine, 1935 and 1975 eras, M332a.

Forest Type Analysis for Mountain Pine Beetle and Western Pine Beetle in Ponderosa Pine in M332a

API analysis

Action probability index (API) data could be calculated for eight of the twelve habitat type/forest type/structure class (HT/FT/SC) combinations occurring in the 1935-era data from 1975-era data in M332a. Five of the eight combinations contained high and/or moderate mountain pine beetle/western pine beetle API values. Three other combinations contained low mountain pine beetle/western pine beetle API values. One of the 12 combinations, one (1/PP/3) did not occur in the 1975-era dataset for M332a but did occur in the 1975-era dataset for M333d. The calculated API values for this combination in M333d contained moderate and high values. The remaining three combinations were not represented in the 1975-era datasets for either M332a or M333d so API data were not available. Due to the small sample size within each of the combinations, this did not impose a serious problem in the analysis.

Observed transitions in forest types with ponderosa pine from 1935 to 1975 eras in M332a

In the 12 HT/FT/SC combinations with the potential for bark beetle activity in ponderosa pine occurring in 1935-era data, ponderosa pine most frequently played a dominant seral role. From these classes, a total of 33 forest type/structure class transitions occurred from the 1935 era to the 1975 era (Figures 6.54 and 6.55). Of these 33, 28 transitions follow the pattern described

by stands impacted by pine bark beetles, i.e., succession was accelerated and/or structure class was changed to smaller trees or lower density. Four transitions had outcomes which were not obviously influenced by bark beetles. In these four transitions, either the beetles were not active, or their impact was overshadowed by other disturbance factors (Table 6.45).

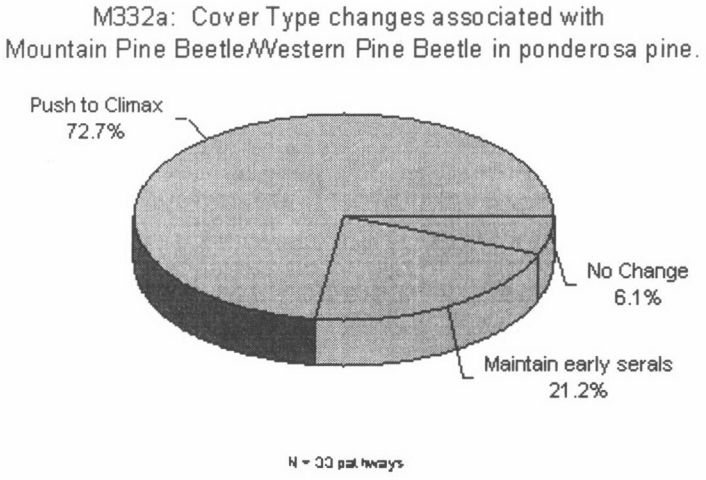

Figure 6.54: Cover type changes associated with mountain pine beetle and western pine beetle in ponderosa pine, M332a.

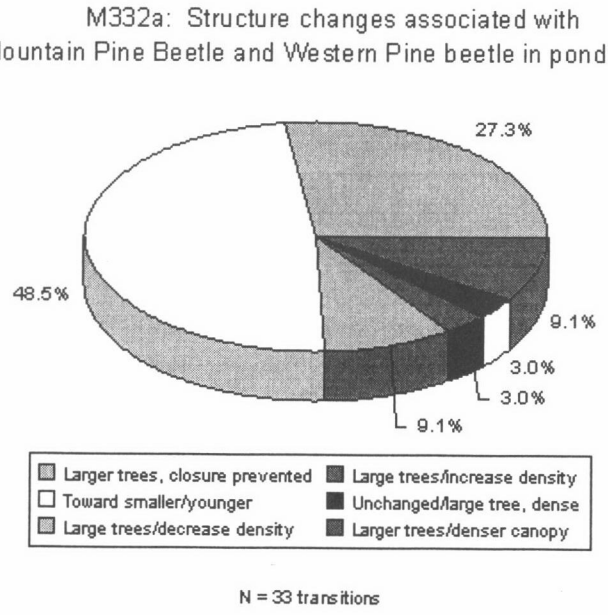

Figure 6.55: Structure changes associated with mountain pine beetle and western pine beetle in ponderosa pine, M332a.

Table 6.45: Transitions in M332a with the Potential for bark beetle Activity.

# Transitions	Percent Affected	Forest Type Effect	Structure Class Effects	Bark Beetle Functions
7	100	Increase climax components	Prevent stand closure	Kill early seral component and reduce stand density
13	100	Increase climax components	Younger/smaller-tree structure	Kill early seral component, removing large trees, leaving younger/smaller components.
1	100	Increase climax components	Increase density	Kill early seral component without affecting stand closure.
3	100	Increase climax components	Normal change to larger trees with moderate to high canopy density	Kill early seral component in mixed stands without significantly altering density or size class.
2	50	Maintain early seral	Prevent stand closure	Kill pine component while reducing stand density and favoring another early seral species
3	67	Maintain early seral	Younger/smaller-tree structure	Kill ponderosa pine while favoring other early seral species and removing most large trees.

2	50	Maintain early seral	Remain large-tree class while increasing density	Kill ponderosa pine while favoring other early seral species but not significantly affecting stand density.
1	0	No change in species	Prevent stand closure	No Bark beetle activity evident
1	0	No change in species	Maintain large-tree, closed canopy structure	No Bark beetle activity evident

For the 29 transitions that were consistent with bark beetle activity, the majority (27) had forest type conversions to types which contained less ponderosa pine. In many cases ponderosa pine went from being a major stand component (i.e. being part of the forest type designation) to being a minor component (not part of the forest type designation). Ponderosa pine was most frequently replaced by Douglas-fir, lodgepole pine, subalpine fir, or cedar.

In two transitions, the structure class changed. In one case (1/DFPP/3 to 1/DFPP/4), the density decreased, and in the other (1/PP/3 to 1/PP/2), the structure class moved from a mature tree structure to a pole stage. Both of these structure class changes are consistent with bark beetle activity which removes larger trees creating openings and encouraging regeneration.

Conclusions for M332a based on forest type analysis

Changes in the abundance of forests containing ponderosa pine are evident from the 1935-era sample and the 1975-era sample (Figure 6.53). Data calculated in the form of bark beetle action probability indices from the 1975-era sample and applied to the 1935-era HT/FT/SC combinations indicate that beetle activity may have played a significant role in the reduction of forest types containing ponderosa pine.

In the 1935-era sample there was significantly more ponderosa pine in mixed forest types than in pure forest types (354 hectares versus 22 hectares, or a 16:1 ratio). All of the pure ponderosa pine forest types were in structure classes 3 and 4; and the vast majority of the mixed ponderosa pine forest types were in these later structure classes as well (328 hectares in SS 3 or 4; 26 hectares in SS 2). Considering the HT/FT/SC of the ponderosa pine forests in the 1935-era sample, all could have supported bark beetle activity.

Although there was a small sample of pure ponderosa pine forest types in the 1935-era sample (22 hectares), the sample size was larger for the mixed ponderosa pine forest types (354 hectares). Of this total of 376 hectares only 30 percent remained in a ponderosa pine forest type (12 hectares pure ponderosa pine and 111 hectares mixed ponderosa pine). The remaining 70 percent transitioned to a more climax forest type (Figure 6.54), as would be expected had bark beetles been active in these HT/FT/SC combinations.

In the 1975-era sample, there were 10 hectares of pure ponderosa pine forest types that had not been classified as pure ponderosa pine in the 1935 era. Of these, six were considered non-forested in the 1935-era sample and four were classified as Douglas-fir forest types. With such a small sample it is difficult to define any trends in the recruitment of pure ponderosa pine forest types. It is possible that the 6 hectares that were considered non-forested had been burned prior to the 1935 era and had not regenerated before the 1935 era. The Douglas-fir recruited into ponderosa pine was in a structure class 4, and converted to a ponderosa pine structure class 4; something which indicates that the ponderosa pine stand is likely not well-stocked and the

Douglas-fir succumbed to another significant disturbance agent between 1935 and 1975 eras leaving the few, remaining ponderosa pine. A larger sample will need to be obtained to identify significant trends in pure ponderosa pine recruitment.

A total of 123 hectares were recruited into mixed ponderosa pine forest types between 1935 and 1975 eras (Figure 6.56). The majority of mixed ponderosa pine forest types were recruited from 1935-era Douglas-fir forest types (93 hectares or 76 percent). This trend from a more shade tolerant species to a more seral species forest type is contrary to what would occur if only vegetational succession was in place, therefore some other disturbance agent- fire or insects and pathogens- are removing the more climax Douglas-fir and giving ponderosa pine a competitive edge in these stands.

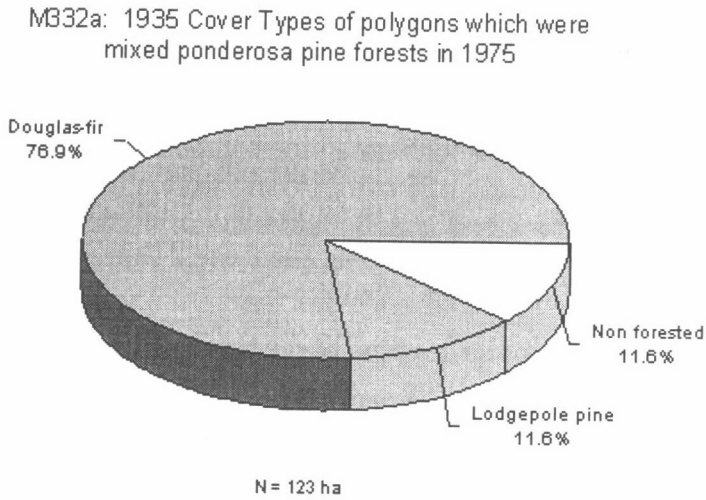
M332a: 1935 Cover Types of polygons which were mixed ponderosa pine forests in 1975
Douglas-fir 76.9%
Non forested 11.6%
Lodgepole pine 11.6%
N= 123 ha

Figure 6.56: 1935-era cover types of polygons that were classified as mixed ponderosa pine forest type in the 1975 era, M332a.

Although the amount of hectares in pure ponderosa pine forest types stayed the same from the 1935-era sample and the 1975-era sample, and a total of 123 hectares of mixed ponderosa pine forest type was recruited, there was still a significant decrease in the amount of hectares containing a significant ponderosa pine component between the 1935-era sample and the 1975-era sample (Figure 6.61). With continued management emphasis on fire exclusion, it is likely that the number of hectares in pure and mixed ponderosa pine forest types will continue to decline. Without fire, ponderosa pine is unable to out compete the more shade tolerant Douglas-fir and true firs that will dominate most stands. Bark beetles will still remain active in ponderosa pine where it exists, however since ponderosa pine is likely to be a smaller component of most stands, the ability of these beetles to cause significant changes in the forest type or structure class of a stand will be significantly reduced.

Cover Type Analysis for Mountain Pine Beetle and Western Pine Beetle in Ponderosa Pine in M333d

API analysis

In the 1975-era sample for M333d, there were 17 habitat type group/cover type/structure class (HT/CT/SC) combinations (polygon classes) which had calculated API values for bark beetles in ponderosa pine. These combinations occurred in habitat type groups 1, 2, 3, 4, and 5 and in cover types 1, 2, 2.8, 5, and 9.

Seven of the 17 polygon classes were represented in the historic data. Of these seven, four had a mixed ponderosa pine cover type, two were white pine cover type, and one was Douglas-fir. For the class with ponderosa pine cover type, all observed transitions were consistent with pine bark beetle effects on succession; i.e., the cover type changed to one with less ponderosa pine and/or the structure class was stalled, moved to an earlier structure class (1 or 2), or stand density was reduced (moved to a SS 4).

Relatively few hectares in the white pine and Douglas-fir cover types were assigned pine bark beetle APIs indicating that the ponderosa pine component mostly fell below the 25 percent requirement for the pine bark beetle API rating. There were a few hectares in these cover types, however, that received high bark beetle API values indicating that stand conditions were highly conducive to bark beetle activity. Bark beetles could have been actively removing the ponderosa pine from these stands, but this activity may not result in a cover type change.

Observed transitions in ponderosa pine cover types (2 and 2.8) from 1935 to 1975 eras

There were 89 observed transitions in polygon classes that had ponderosa pine cover types (2.8 or 2) in the 1935 era. In that sample, 1,169 hectares had ponderosa pine cover types. Of these, 23 percent were pure ponderosa pine type, and 77 percent were mixed ponderosa pine cover type. In the 1975 era, only 375 hectares had ponderosa pine cover types. Of these, 35 percent were relatively pure ponderosa pine, and 74 percent were mixed ponderosa pine type (Figure 6.57). All of the hectares in ponderosa pine cover types in the 1975 era were ponderosa pine cover types in the 1935 era, i.e., no ponderosa pine cover types were recruited from other cover types. One hundred and six hectares of ponderosa pine cover type transitioned from pure ponderosa pine in the 1935 era to mixed ponderosa pine in the 1975 era. On 47 hectares, the cover type went the opposite direction; from a mixed in the 1935 era to a pure pine in the 1975 era. It is unlikely that pine bark beetles were active in these stands.

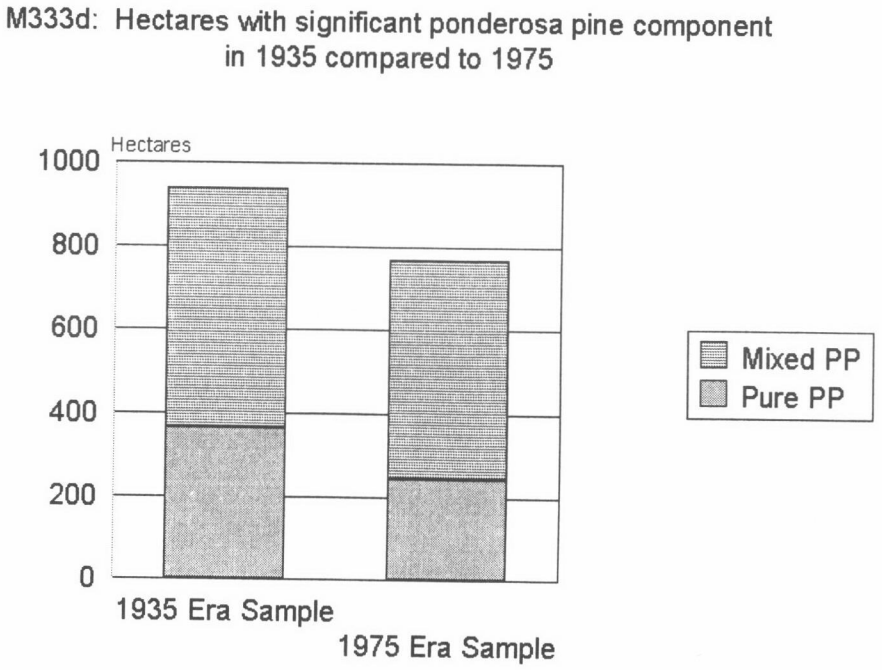

Figure 6.57: Hectares with significant ponderosa pine component, 1935-era and 1975-era, M333d.

Of the 1,169 hectares of ponderosa pine in the 1935 era, 32 percent stayed in ponderosa pine cover types, 20 percent transitioned Douglas-fir cover type, 11 percent went to grand fir, 9 percent changed to lodgepole pine cover type, 8 percent became non-forested, 7 percent became larch/Douglas-fir mixture, 6 percent went to cover type 11 (subalpine fir or mountain hemlock), 4 percent to western white pine and the remaining 3 percent became cedar/grand fir, or hemlock/grand fir (Figures 6.58 and 6.59).

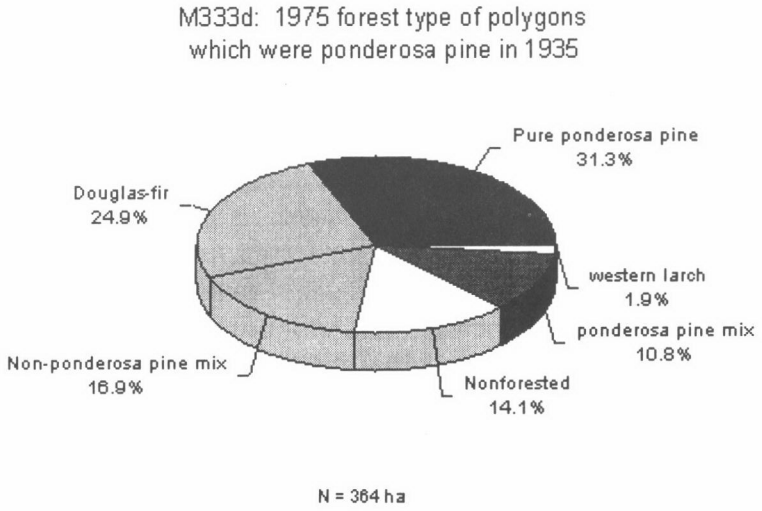

Figure 6.58: 1975-era forest types of polygons that were ponderosa pine in the 1935 era, M333d.

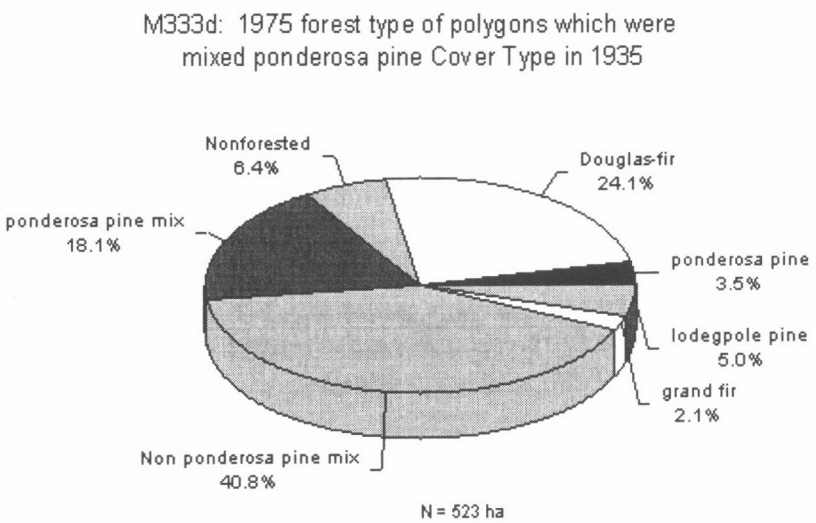

Figure 6.59: 1975-era forest types of polygons that were mixed ponderosa pine in the 1935 era, M333d.

There were significant changes in the structure class distribution between ponderosa pine cover types from the 1935 era to the 1975 era. In the 1935 era, approximately 54 percent (627 hectares) of ponderosa pine cover types were in structure class 4, 8 percent (94 hectares) were in structure class 3; and 38 percent (448 hectares) were in structure class 2. In the 1975 era, 49

percent of forests with ponderosa pine cover types were in structure class 2 (185 hectares); 29 percent (110 hectares) were in structure class 4; 13 percent (47 hectares) were in structure class 3; and 9 percent (33 hectares) were in structure class 1 (Figure 6.60). The biggest change is the increase in the proportion of ponderosa pine cover types in structure classes 2 and 3 (from 8 percent and 0 in the 1935 era to 49 percent and 13 percent in 197,5 respectively).

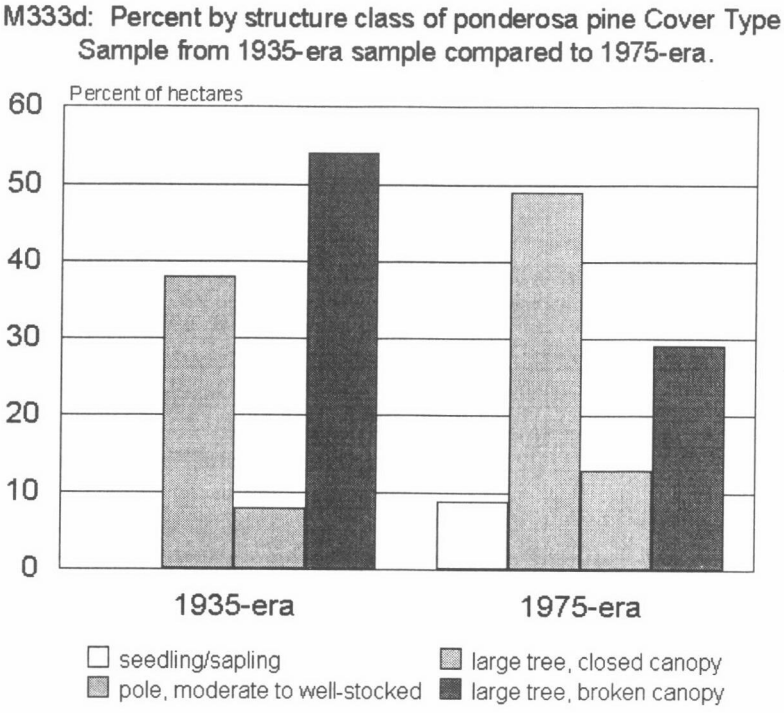

Figure 6.60: Percentages by structure class of ponderosa pine cover type, 1935 and 1975 eras, M333d.

Most of the transitions in ponderosa pine cover type in the 1935 era were consistent with mountain pine beetle or western pine beetle activity (Table 6.46). In terms of area, 77 percent (900 hectares) of ponderosa pine cover type in the 1935-era sample transitioned to a different cover type indicating that ponderosa pine abundance was reduced to below 25 percent of the stand, potentially by bark beetle activity (Figures 6.58 and 6.59). Nineteen percent of the sample stalled (i.e., succession did not move forward), and 39 percent moved backward to a smaller/younger structure class. This is consistent with bark beetle activity removing larger diameter trees. In 37 percent of the 1935-era ponderosa pine cover type hectares, structure class changes were consistent with bark beetle activity, removing a portion of the trees creating openings or low-density canopy conditions (Figure 6.59).

The remaining 9 percent of the 1935-era ponderosa pine cover type hectares (112 hectares) experienced transitions which were contrary to what would be expected if bark beetles were active. On these hectares either beetles were not active or their impact was overshadowed by other disturbance factors.

Table 6.46: Cover type changes of polygons in M333d which had high potential for effects from bark beetles in ponderosa pine.

# Transitions	Successional Impact	Bark Beetle Functions
71	Increase climax components without affecting structure	Killing ponderosa pine component resulting in conversion to another cover type with less ponderosa pine.
4	No successional change observed- Stalled	MBP/WPB activity may have prevented succession from moving forward by removing larger ponderosa pine and preventing canopy closure
3	Largest trees die; move toward young, small tree components	Kill the large-diameter ponderosa pine in structure classes 3 and 4, resulting in shift to young and small trees (SCs 1 and 2).
3	Reduce density without changing the cover type	Structure classes changed from 2 or 3 to 4. Bark beetles killed ponderosa pine components, creating openings in the canopy, preventing closure.
8	Successional changes contrary to what would be expected if pine bark beetles were very active	Either pine bark beetles were not active in these transitions or their impacts were overshadowed by other factors, such as silvical succession or other disturbance agents

Conclusions for M333d based on cover type analysis

Cover type analysis indicated a 68 percent reduction in the number of hectares occupied by ponderosa pine cover types from the 1935 era to the 1975 era (Figure 6.57). The cover type analysis also indicated that ponderosa pine cover types were not recruited from other forest types, and that more of the pure ponderosa pine cover types in the 1935-era sample converted mixed ponderosa pine cover type in the 1975-era sample, than mixed converting to pure (106 hectares went from 2.8 to 2 compared to 47 hectares going from 2 to 2.8). The changes in amount of ponderosa pine cover type and relative proportion of pure and mixed ponderosa pine cover types are likely the result of lack of fire and bark beetle activity between the 1935 era and the 1975 era. Ponderosa pine cover types, especially pure ponderosa pine cover types, are the most susceptible to bark beetle-influenced successional changes.

Forest Type Analysis for Mountain Pine Beetle and Western Pine Beetle in Ponderosa Pine in M333d

API analysis

Action probability index (API) data could be calculated for 14 of the 23 HT/FT/SC combinations occurring in the 1935-era sample. Nine of the 14 combinations contained high or

moderate mountain pine beetle/western pine beetle API values. Of these nine, seven did not have ponderosa pine in the forest type definition (i.e., ponderosa pine was not among to top three species based on plurality of basal area). Four other combinations were assigned low mountain pine beetle/western pine beetle API values.

Observed transitions in forest types with ponderosa pine from the 1935 era to the 1975 era

In the 23 HT/FT/SC combinations with the potential for bark beetle activity in ponderosa pine occurring in 1935-era sample, ponderosa pine most frequently played a dominant seral role in habitat type groups 1 and 2; and a minor seral role in habitat type groups 3, 4, and 5. A total of 85 forest type/structure class transitions occurred from the 1935-era sample to the 1975-era sample (Figures 6.61 and 6.62). Of these, only 41 were consistent with bark beetle activity; i.e., there was a push to climax forest type and/or there was a structure class change consistent with beetle impacts. In 44 transitions there was no obvious bark beetle influence. In a large number of the transitions observed, high and moderate API values were calculated for the HT/FT/SC combinations in spite of the fact that ponderosa pine was never considered a significant enough component of the stand to be incorporated into the forest type designation. For these transitions it is not possible to determine what, if any effect bark beetles may have had on the ponderosa pine component of the stand.

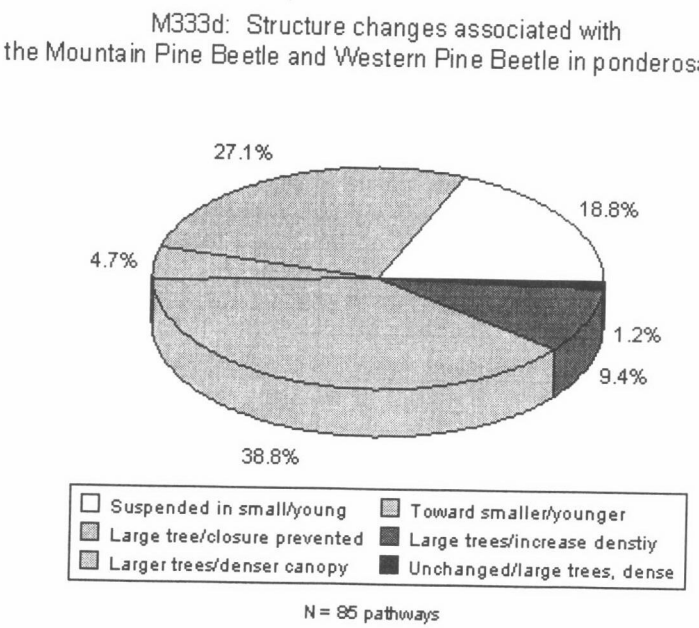

Figure 6.61: Structure changes associated with mountain pine beetle and western pine beetle in ponderosa pine, M333d.

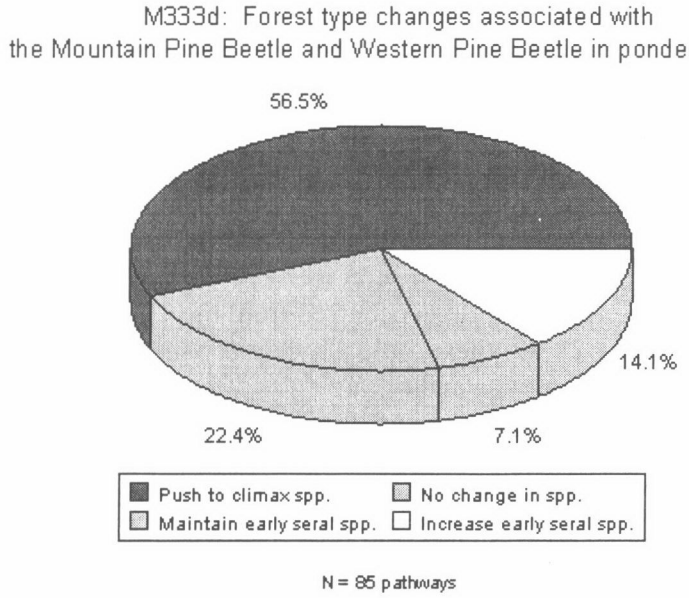

Figure 6.62: Forest type changes associated with mountain pine beetle and western pine beetle in ponderosa pine, M333d.

Table 6.47: Transitions in M333d with the Potential for bark beetle Activity.

# Transitions	Percent Affected	Impact on Forest type	Impact on Structure class	Bark Beetle Functions
10	30	Increase climax components	Stalled in pole-size	Killing the larger ponderosa pine component favoring smaller, more climax components.
15	73	Increase climax components	Prevent stand closure	Killing some of ponderosa pine component, while reducing stand density.
2	50	Increase climax components	Normal change to larger trees with moderate to high canopy density	Killing enough ponderosa pine to shift cover type to climax components, without significantly reducing density.
15	80	Increase climax components	Younger, smaller-tree structures	Killing larger ponderosa pine components leaving smaller, more climax composition.
5	20	Increase climax components	Large-tree structure; increase in stand density	Killing enough ponderosa pine to change cover type without significantly reducing stand density.

5	60	Maintain early seral	Prevent stand closure	Killing ponderosa pine results in reduced stand density and favoring other early seral species.
2	50	Maintain early seral	Normal change to larger trees with moderate to high canopy density	Killing ponderosa pine, favors shift to other early seral components without significantly reducing stand density.
8	88	Maintain early seral	Younger, smaller-tree structures	Killing larger ponderosa pine component shifts structure to smaller trees and favors other early seral components.
8	25	Initiate early seral	Younger, smaller-tree structures	A relatively pure stand of ponderosa pine is mostly killed, resulting in stand regeneration to early seral species.

For the 41 transitions that were consistent with bark beetle activity, the majority (34) had forest type conversions to more shade-tolerant species or other non-ponderosa pine early seral species. In many cases, ponderosa pine went from being a major stand component (i.e. being part of the forest type designation) to being a minor component (not part of the forest type designation). Ponderosa pine was most frequently replaced by Douglas-fir.

In seven transitions, forest type did not shift dramatically: however, in three transitions closure was prevented and in four transitions an earlier structure class was initiated. Bark beetles may cause both of these structural stage impacts by removing large trees creating openings in the canopy (preventing canopy closure) and encouraging regeneration (invoking an earlier structural stage).

Conclusions based on forest type analysis of M333d

Changes in the nature and size of forests with a significant ponderosa pine component are evident in M333d (Figure 6.57). Data calculated in the form of bark beetle APIs from the 1975-era sample and applied to the 1935-era polygon classes show that bark beetles may have played a significant role in some of the changes observed forests with a component of ponderosa pine. Also, the transitions which occurred in the 1935 era were consistent with what would have been predicted had bark beetles been active.

In the 1935-era sample there were approximately 364 hectares of pure ponderosa pine forest types and 523 hectares of mixed ponderosa pine forest types. By the 1975-era sample. the total number of hectares occupied by ponderosa pine forest types had dropped approximately 18 percent (from 940 hectares to 769 hectares) and the ratio of pure ponderosa pine to mixed ponderosa pine forest types had dropped from .63 to .46. These changes in the size and nature of the ponderosa pine containing forests is consistent with a reduction in fire frequency and bark beetle activity.

Approximately 69 percent (251 hectares) of the forests that were considered pure ponderosa pine forest types in the 1935-era sample transitioned to other forest types by the 1975-era sample (Figure 6.66). Most of the pure ponderosa pine converted to more climax forest types, as would be expected given the success of fire suppression efforts between the sample

dates. During that time, 113 hectares of pure ponderosa pine forest types were recruited from other forest types (Figure 6.63). Most of the recruited pure ponderosa pine (70 percent) came from areas considered nonforested in the 1935 era. These areas were mostly classified as recently burned in the 1935-era survey. With the current emphasis on fire suppression, it is unlikely that similar reservoirs of land exist which may become ponderosa pine forests. An additional 14 hectares (12 percent) came from white pine forest types, a possible result of white pine blister rust killing white pine and limiting its regeneration, allowing ponderosa pine to gain an competitive edge on these sites. Since the white pine forests have already experienced a major decline due to blister rust, it is unlikely that significant amounts of pure ponderosa pine forests will be recruited from white pine forest types in the future. The remaining 20 hectares (18 percent) came from larch and Douglas-fir larch forests. The conversion of larch and Douglas-fir/larch forests into ponderosa pine forest types is inconsistent with succession, so some other disturbance factor must have been involved.

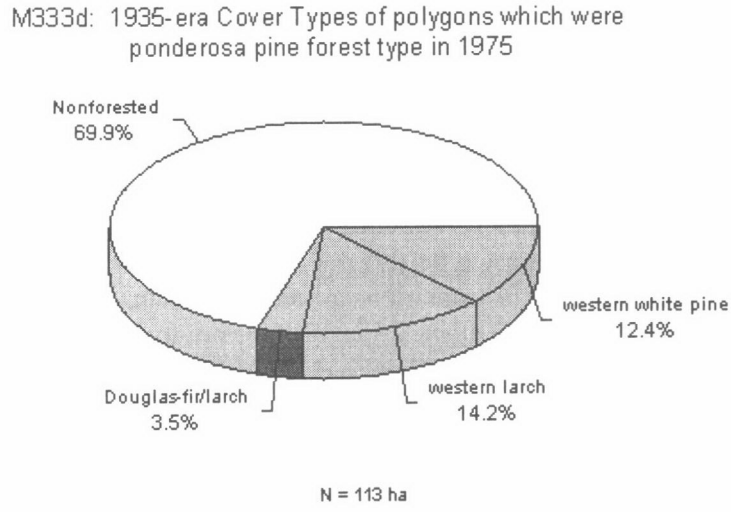

Figure 6.63: 1935-era cover types of polygons that were pure ponderosa pine forest type in 1975-era, M333d.

Approximately 79 percent (411 hectares) of forests that were considered mixed ponderosa pine forest types in the 1935-era sample transitioned to another forest type by the 1975-era sample (Figure 6.59). Most of the mixed ponderosa pine converted to more climax forest types, as would be predicted given the emphasis on fire suppression during the 40 years between samples. During that time, 392 hectares of mixed ponderosa pine forest types were recruited from other forest types (Figure 6.64). Of the 392 hectares, 252 (64 percent) were recruited from areas considered non forested in the 1935 era. These areas were probably burned at some time prior to the 1935 era and had not regenerated to the point of being considered forested. With the current emphasis on fire suppression, it is unlikely that similar reservoirs of land exist which may become mixed ponderosa pine forests. The remaining 140 hectares (36 percent) came from Douglas-fir, larch, Douglas-fir/larch, Douglas-fir/lodgepole, and Douglas-

fir/grand fir/larch forests. The conversion these forest types into mixed ponderosa pine forest types is inconsistent with succession, so some other disturbance factor must have been involved.

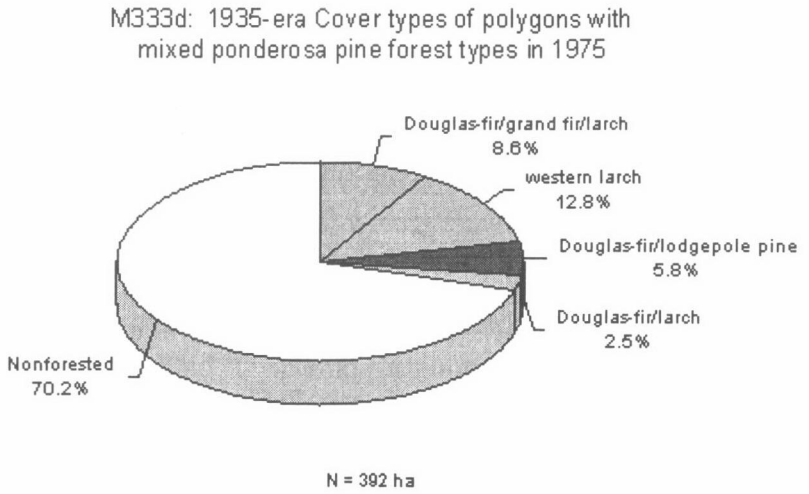

Figure 6.64: 1935-era cover types of polygons that were mixed ponderosa pine forest type in the 1975 era, M333d.

The data for M333d shows a decreasing trend in ponderosa pine abundance from the 1935 to 1975 eras. This trend is most likely the result of fire suppression, which gives ponderosa pine a competitive advantage on sites where it plays a seral role, and of bark beetle activity, which kills pole-size and larger ponderosa pine trees. Without periodic fire to give ponderosa pine a competitive advantage, it is unlikely that the amount of forests with a significant ponderosa pine component will increase in the near future. As the amount of ponderosa pine decreases across the landscape, so will the influence of bark beetles that attack it.

MOUNTAIN PINE BEETLE SUCCESSION FUNCTIONS IN WESTERN WHITE PINE AND WHITEBARK PINE

By Sandra Kegley

Historic Role Up to the 1935 Era

The mountain pine beetle was very prominent and played a significant role in historic western white pine forests. Beetle outbreaks were described and control attempted in the early 1900s (Evenden 1915, 1921, 1924; Terrell 1930, 1932). White pine stands became susceptible to mountain pine beetle attack when they reached about 70 years of age. However, the highest mortality rates occurred in stands that were greater than 160 years old (Terrell 1961). Stand density was also an important factor. The beetle was most successful in killing trees in dense stands with basal areas greater than 180 square feet per acre (Terrell 1961). Historically, the proportion of western white pine was quite high (40-60 percent) in many white pine stands (Terrell 1961) compared to what is left today. Major mountain pine beetle outbreaks probably occurred during or following periods of drought when warm, dry weather conditions were conducive to beetle development and trees were moisture stressed. Drier than average conditions occurred near Spokane, Washington, from 1916-1926 and 1928-1939 (National Weather Service data, Spokane, WA), coinciding with historic reports of major beetle outbreaks on the nearby Coeur d'Alene National Forest. Beetles could kill the majority of large, mature white pine in a stand within a few years' time. Their action changed the forest type from white pine to other tree species (western redcedar, western hemlock, grand fir, Douglas-fir, and western larch). Since white pine is seral on all habitat types where it grows, the loss of white pine would either accelerate forest succession to a more climax species composition or change to other early seral tree species. Forest structure class was also affected by mountain pine beetle killing mature white pine. Their activity opened up stands changing from a mature closed canopy (structure class 3) to an open canopy (structure class 4), decreasing stand density. Beetles may also have affected a forest in structure class 4 by continually killing trees and opening the canopy, keeping it in a class 4, preventing canopy closure. In cases where large groups of white pine were killed, mountain pine beetle could have caused a transition to a structure class 1 or 2 (seedling, sapling, or pole) or predisposed the stand to fire, resetting succession and allowing new seedlings to become established (changing stands to an earlier structure class) (Figure 6.65). Where white pine grows in mixed forests with forest types other than white pine, mountain pine beetle may kill the white pine in the stand but the affect may not cause a transition in forest succession.

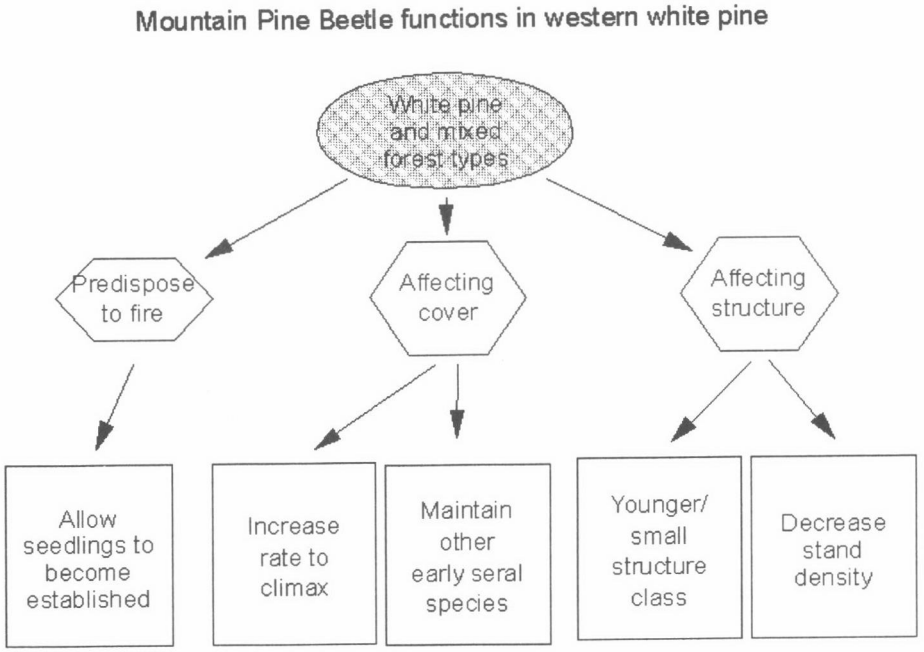
Mountain Pine Beetle functions in western white pine
White pine and mixed forest types
Predispose to fire
Affecting cover
Affecting structure
Allow seedlings to become established
Increase rate to climax
Maintain other early seral species
Younger/ small structure class
Decrease stand density

Figure 6.65: Mountain pine beetle functions in western white pine.

Role of Mountain Pine Beetle from the 1975 Era to the Present

Currently, mountain pine beetle has similar functions in remaining old growth white pine, but on a much smaller scale. However, some differences do occur since there is less mature white pine. Very large groups of white pine are not available to be killed, so the beetle probably does not reset succession. Small groups and individual mature trees are killed, pushing the forest to a more climax species composition. We have some evidence from 1995-1997 surveys that show mountain pine beetle is now causing significant mortality in second-growth western white pine of a much younger size and age class (10-12 inches in diameter and 60 years old, or pole-sized stands) than those typically infested in the past. Sometimes these trees are also infected with white pine blister rust or root disease. Mountain pine beetle may now play a larger role in pole-sized white pine forests where it was not as active in the past because there is a lot less older, mature white pine available for the beetle to colonize. The most likely change would be from a pole structure class (2) to an open canopy (structure class 4) with a change in forest type from white pine to a climax tree species or other early seral species such as larch or Douglas-fir.

Statistics from M332a

Action probability index values

The highest action probability index (API) found in M332a (from 1975-era stand data) occurred in white pine forest type, structure class 3 (closed canopy mature) in habitat type group 5 (moderately cool and moist) (Table 6.48). More moderate values were found in other forest types (such as grand fir, Douglas-fir, cedar, subalpine fir and mountain hemlock), structure

classes 3 and 4, in habitat type groups 5 and 7. White pine forest type, structure class 3, habitat type group 7 was also moderate.

Table 6.48. Mountain pine beetle in white pine (WP) Action Probability Index values for habitat type group, forest type, structure class combinations in ecosection M332a (based on 1975-era stand data).

HT Group	Forest Type	Structure Class	API	Frequency of API
5	WP	3	H	100%
5	C	3	H	14%
5	C	3	M	14%
5	DFGF	3	M	64%
5	GF	3	M	37%
7	AFCDF	3	M	100%
7	AFDFS	3	M	84%
7	MH	4	M	87%
7	WP	3	M	100%

Mountain pine beetle APIs occurred in a few polygons with whitebark pine as the primary white pine species (Table 6.49). The sample of these types was very small, however, with only 135 hectares of whitebark pine type assigned APIs greater than 0 for mountain pine beetle. This is too small a sample to evaluate successional effects. General trends do, however, appear to be similar to those found in western white pine types with respect to the declining role of mountain pine beetle.

Table 6.49. Mountain pine beetle in whitebark pine (WB) API values for habitat type group, forest type, structure class combinations in ecosection M332a (based on 1975-era stand data).

HT Group	Forest Type	Structure Class	API	Frequency of API
7	AFS WB	2	M	100%
9	AFWB	4	M	100%
9	WB	2	H	100%
9	AFLP	2	M	27%
9	AF	2	M	12%
10	AFS	2	M	34%

Transition probabilities

Many of these habitat type group/forest type/structure class combinations (HT/FT/SC) did not exist in our 1935-era data, so we have little transition data to analyze in this ecosection. Some transitions occurred in white pine where we had no 1975-era data to calculate mountain pine beetle API values. However, the transitions logically could have been caused by mountain pine beetle, and we have moderate to high 1975-era API values from ecosection M333d to support our assumptions. For example, in habitat type group 4 (moderately warm and moist), white pine forest type, structure class 3, 39 percent changed forest type (Increase climax components) and went to an earlier structure class (DFGF structure class 1). The mountain pine beetle could certainly have killed a large proportion of the white pine and changed both the forest type and structure class. This type of transition was rated as having a high probability of occurring due to mountain pine beetle (Table 6.50). The other 61 percent of that HT/FT/SC went to non-forest but had a high amount of forest management so no mountain pine beetle API was assigned. The same transition functions occurred in habitat type group 9, white pine forest type, structure class 3 where mountain pine beetle most likely caused an increase climax components and earlier structure class transition (100 percent went to AF2) but with a moderate probability based on other mountain pine beetle API values in habitat type group 9. In habitat type group 4, white pine forest type, structure class 4, 46 percent changed forest type (increase climax components species) and transitioned to an earlier structure class (DFGF1, DFGFL2), 45 percent changed forest type (increase climax components) and stayed structure class 4 (prevented canopy closure) (DFGF4) and 9 percent changed to Non-forest. The non-forest transition had a high amount of management and no mountain pine beetle API was assigned. The other transitions could have occurred due to the mountain pine beetle but with a moderate probability based on API values in structure class 4 in other habitat type groups (Table 6.50). Mountain pine beetle also could have caused similar transitions with a moderate probability in habitat type group 7, AFDFWP forest type, structure class 4, where 23 percent went to MH 4 (increase climax components and prevent canopy closure functions). There are several forest types other than WP that had mountain pine beetle API values but the transitions that occurred were not logically caused by mountain pine beetles. These were assigned a low probability of occurring due to mountain pine beetle (Table 6.50). A summary of mountain pine beetle transitions in ecosection M332a is shown in Figure 6.66.

Table 6.50. Transitions occurring in M332a with low, moderate, or high probabilities due to mountain pine beetle.

HT Grp	Start FT	Start SS	End FT	End SS	MP-BWP prob	Path ha	% Path	Cover Trans.	Struct. Trans.
4	WP	3	DFGF	1	H	15	39	CC	ES
4	WP	4	DFGF	1	M	11	24	CC	ES
4	WP	4	DFGF	4	M	28	61	CC	PC
4	WP	4	DFGFL	2	M	3	7	CC	ES

5	C	3	C	3	L	70	100	MM	NN
5	DFGF	3	C	3	L	12	100	CC	MM
5	GF	3	CGF	3	L	28	61	CC	MM
5	GF	3	GF	3	L	7	15	MS	MM
5	GF	3	GF	4	L	12	26	MS	DD
7	AFDFS	3	MH	3	L	3	100	CC	MM
7	AFDFWP	4	AFDFS	3	L	7	9	CC	ID
7	AFDFWP	4	AFGFS	3	L	39	52	CC	ID
7	AFDFWP	4	DFMHS	3	L	12	16	CC	ID
7	AFDFWP	4	MH	4	M	17	23	CC	PC
9	WP	3	AF	2	M	4	100	CC	ES

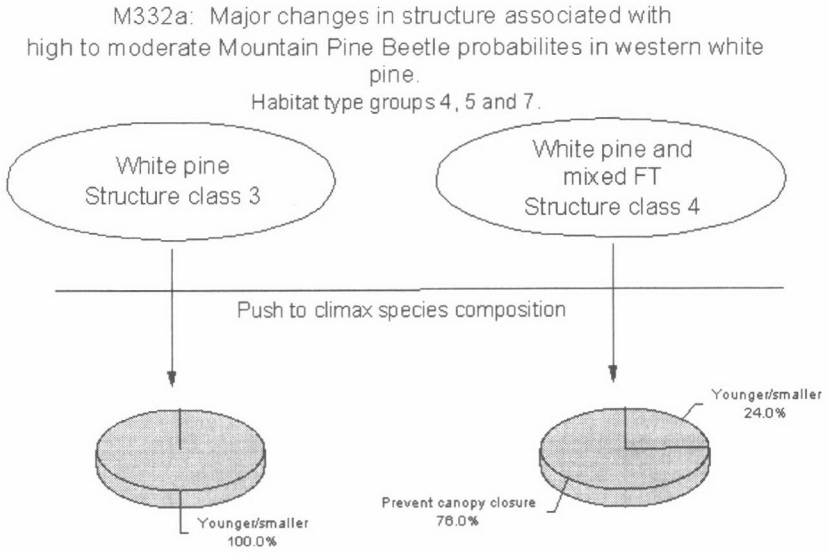

Figure 6.66: Major changes in structure associated with high to moderate mountain pine beetle probabilities in western white pine, M332a.

Statistics from M333d

API values

The highest mountain pine beetle in white pine API values (based on 1975-era data) occurred in white pine forest types, mature closed canopy (SC 3) stands, on habitat type groups 4, 5, and 7 (Table 6.51). Some high values also occurred in mature closed canopy stands, habitat type groups 4, 5, and 7, and forest types of cedar, mountain hemlock, grand fir, Douglas-fir and various combinations of those tree species. Moderate values occurred in habitat type groups 4, 5, 7, and 9, structure classes 2, 3, and 4 (although the vast majority were in structure classes 3 and 4), in forest types subalpine fir, cedar, Douglas-fir, grand fir, mountain hemlock, western hemlock, spruce, larch, lodgepole pine, and various combinations of those tree species.

Table 6.51. Mountain pine beetle in white pine (WP) API values for habitat type group, forest type, structure class combinations in ecosection M333d (based on 1975-era stand data).

HT Group	Forest Type	Structure Class	API	Frequency of API
4	AFDFGF	4	H	65%
4	DFGF	3	H	34%
5	WP	3	H	100%
5	MH	3	H	100%
5	GFL WH	3	H	84%
5	C DFWH	3	H	80%
5	C	3	H	61%
5	GFWH	3	H	45%
7	C GFS	3	H	100%
7	DFGFWP	3	H	100%
7	WP	3	H	100%
7	AFDFMH	3	H	40%

Polygons with whitebark pine composition were rated for mountain pine beetle action probability as well (Table 6.52). Relatively few hectares (407) had APIs of moderate to high in the 1975 era. There was probably substantially more whitebark pine in the 1935 era. There are a few records of large outbreaks of mountain pine beetle in whitebark pine in the 1930s and 1940s.

Between these outbreaks and white pine blister rust, little remains of the mature whitebark pine forests of the past. Our data are insufficient to assess the changes in this type. The cover types assigned to forests most likely to contain whitebark pine in the 1935 era were too general to discern whether whitebark pine was present or not, falling primarily into the "Alpine" class.

Table 6.52. Mountain pine beetle in whitebark pine (WBP) API values for habitat type group, forest type, structure class combinations in ecosection M333d (based on 1975-era stand data).

HT Group	Forest Type	Structure Class	API	Frequency of API
9	AFMHWB	2	H	100%
9	AFWB	2	H	100%
9	AFWB	4	H	100%
7	MH	2	M	27%
7	AFMH	2	M	25%
7	AFMH	2	M	25%
7	MH	3	M	23%
7	AFMHS	2	M	19%
9	AFDFMH	4	M	100%
9	AFDF	2	M	46%
9	AFMH	2	M	26%
9	AF	4	M	25%
10	AFLPWB	2	M	100%
10	AFMHS	3	M	100%
11	AF	1	M	77%

Transition probabilities

There were many HT/FT/SC combinations with high mountain pine beetle API values for which we did not have 1935-era data to analyze transitions. The transitions that occurred for which we had 1935-era data, and where mountain pine beetle had high API values, occurred in habitat type groups 5 and 7, white pine forest types, structure class 3. High probability values were given to those transitions where both forest type and structure class changed from 1935 to

1975 eras (Table 6.53), moderate values were assigned where forest type changed but structure class did not (Table 6.54), and low values were assigned where white pine remained in the forest type in combination with other tree species (Table 6.55). In habitat type group 5, only 8 percent of the area remained a white pine forest type with other tree species, structure class 3, and was rated low for mountain pine beetle. The rest changed forest type to cedar, Douglas-fir, grand fir, western hemlock, and various combinations of species. About 60 percent of those stayed in structure class 3 and were rated as moderate for mountain pine beetle to cause those transitions. About 14 percent changed to structure class 2 or non-forest (earlier structure class) and 18 percent changed to structure class 4 (decrease density) and were rated high for mountain pine beetle. In habitat type group 7, all of white pine forest type, structure class 3 transitioned to a different forest type (cedar, grand fir, mountain hemlock, spruce and various combinations) (100 percent increase climax components). About 43 percent remained a structure class 3 and was rated moderate for mountain pine beetle. About 15 percent changed to structure class 2 (earlier structure class) and 42 percent changed to a structure class 4 (decrease density) and was rated high for mountain pine beetle.

In habitat type group 7, white pine forest type, structure class 4, the API value for mountain pine beetle was mostly moderate. All of this type transitioned to other forest types (86 percent increase climax components, 14 percent maintained other early seral species). The majority of the type increased density to a structure class 3 and a low value for mountain pine beetle causing the transition was assigned. About 12 percent changed to structure class 2 and 6 percent remained a 4 and a moderate value for mountain pine beetle causing these transitions was assigned based on the API value.

We had no 1975-era data for some mixed forest types with a white pine component in structure class 3 in habitat type groups 4 and 5. In all cases, white pine dropped out of the species mix. Although mountain pine beetle likely played a role in causing these transitions, all were given a moderate mountain pine beetle probability value because we had no current data to calculate API values. For our summaries, moderate and high mountain pine beetle probabilities are treated the same so these transitions are included in those most likely caused by mountain pine beetle (Figures 6.67 and 6.68).

Table 6.53. Transitions occurring in M333d with a high mountain pine beetle probability.

HT Group	Start FT	Start SC	Cover Transition	Structure Transition	Number of Hectares
5	WP	3	CC	DD	113
5	WP	3	CC	ES	28
5	WP	3	IS	ES	4
5	WP	3	MS	ES	29
7	WP	3	CC	DD	22
7	WP	3	CC	ES	8

Table 6.54. Transitions occurring in M333d with a moderate mountain pine beetle probability.

HT Group	Start FT	Start SC	Cover Transition	Structure Transition	Number of Hectares
4	DFGF	4	CC	ES	6
4	DFGF	4	CC	PC	9
4	DFGF	4	MM	PC	44
4	DFGFL	4	CC	ES	4
4	DFGFWP	3	CC	DD	2
4	DFGFWP	3	CC	ES	18
4	DFGFWP	3	CC	MM	2
4	GFWHWP	3	CC	NN	1
4	GFWHWP	3	IS	DD	2
4	GFWHWP	3	IS	ES	16
4	GFWP	3	CC	MM	1
4	GFWP	3	IS	ES	3
5	GFWP	3	CC	DD	102
5	GFWP	3	CC	MM	87
5	GFWP	3	MS	MM	20
5	WP	3	CC	ES	29
5	WP	3	CC	MM	320
5	WP	3	MS	MM	42
7	WP	3	CC	MM	23
7	WP	4	CC	ES	27
7	WP	4	CC	PC	16
7	WP	4	MS	ES	7

Table 6.55. Transitions occurring in M333d with a low mountain pine beetle probability.

HT Group	Start FT	Start SC	Cover Transition	Structure Transition	Number of Hectares
4	DFGF	4	MM	ID	16
4	DFGFL	4	CC	PC	27
5	DFGFL	3	CC	MM	6
5	DFGFWH	4	CC	ES	33
5	DFGFWH	4	IS	PC	4
5	DFGFWH	4	MS	ID	14
5	GFWP	4	CC	ES	56
5	GFWP	4	CC	ID	506
5	GFWP	4	CC	PC	136
5	L	2	CC	PC	2
5	WP	3	CC	MM	63
7	WP	4	CC	ID	234
9	AFLS	4	CC	ES	2

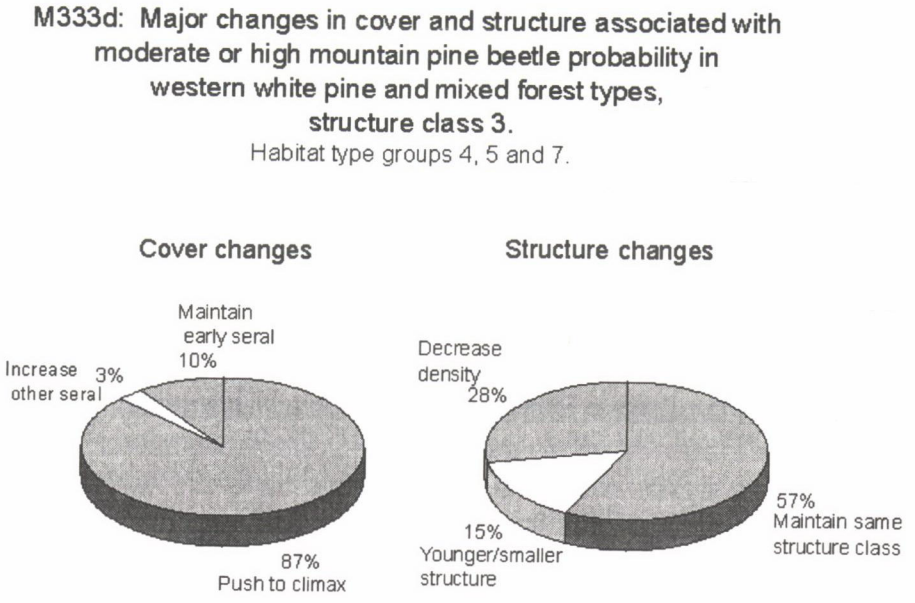
M333d: Major changes in cover and structure associated with moderate or high mountain pine beetle probability in western white pine and mixed forest types, structure class 3.
Habitat type groups 4, 5 and 7.
Cover changes
Structure changes
Maintain early seral 10%
Increase other seral 3%
87% Push to climax
Decrease density 28%
57% Maintain same structure class
15% Younger/smaller structure

Figure 6.68: Major changes in cover and structure associated with moderate to high mountain pine beetle probability in western white pine and mixed forest types, structure class 3, habitat type groups 4, 5, and 7 in M333d.

Overall Status Within the Sample

The amount of mature white pine in both M332a and M333d was relatively small compared to the overall sample. Transitions occurring in M332a that were attributed to mountain pine beetle with high or moderate probabilities covered 78 hectares, 2 percent of the total sample area.

High or moderate mountain pine beetle in white pine probabilities in M333d were assigned to 899 hectares, or 5 percent of the total sample. However, high or moderate probabilities occurred in 13 percent of the total sample of forest types in structure classes 3 and 4, which were the structure classes in which the vast majority of mountain pine beetle APIs occurred.

Comparisons Between M332a and M333d

Mountain pine beetle acting in white pine had a much greater effect in ecosection M333d than M332a, probably because there was much more mature white pine in M333d. However, transitions that occurred were similar between the two ecosections. In most cases, mountain pine beetle caused forest type to change from white pine to other tree species and caused structure class to change from a 3 to a 2 or 4.

M333d: Major changes in cover and structure associated with moderate or high mountain pine beetle probability in western white pine and mixed forest types.
Habitat type groups 4, 5 and 7.

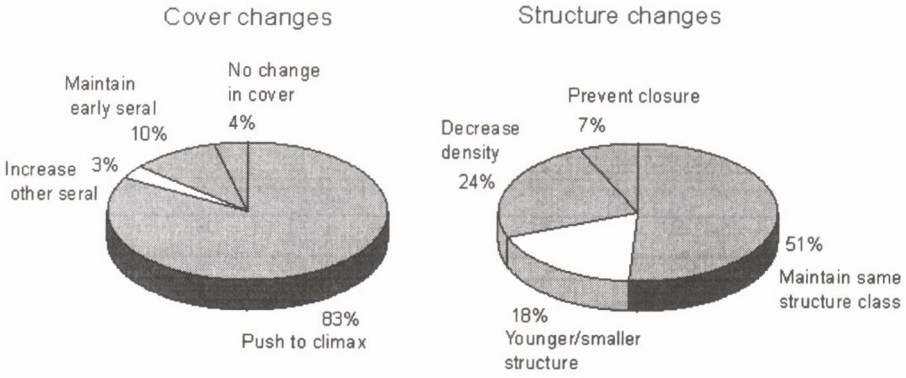

Figure 6.67: Major changes in cover and structure associated with moderate to high mountain pine beetle probability in western white pine and mixed forest types, habitat type groups 4, 5, and 7 in M333d.

Ecological Implications

The most important function (or the function that occurred most frequently) of mountain pine beetle in mature western white pine was to change forest type, pushing the forest to a more climax tree species. The second most abundant transition was to change structure class from a mature forest (class 3) to a mature open forest (stage 4), decreasing density, or from a stage 3 to a 2 or 1, resetting to an earlier structure class.

Since the mountain pine beetle is a native insect, and has co-evolved with western white pine, these are natural functions. However, the extent and proportion of these functions has changed over time. In historic white pine forests, mountain pine beetle probably played a much larger role in resetting succession or predisposing the forest to fire, allowing white pine to regenerate. With the introduction of white pine blister rust, younger classes of white pine are killed before they can mature. Blister rust affects combined with fire suppression produce an end result of an overall change in forest type away from white pine. Mountain pine beetle in white pine has declined in abundance with the decline in mature white pine and there are less large white pine snags available for wildlife. However, mountain pine beetle still may be playing a very important role in removing the last natural blister rust resistant mature western white pine and, therefore, the last remaining natural resistant seed source.

We have yet to learn the extent of the role mountain pine beetle will play in younger, second-growth white pine forests. We have some evidence that it currently attacks younger trees than it has in the past and often these trees are infected with blister rust or root disease. The beetle may weed out diseased trees and populations may stay low so that it's role would be a thinning agent. It is possible that diseased trees may be a continual source of beetles, allowing populations to expand rapidly during periods of drought, with outbreaks occurring in second growth white pine, similar to what now occurs in lodgepole pine, allowing the beetle to reset forest succession to a younger structural class. In mixed stands, mountain pine beetle will probably continue to weed out individual and small groups of mature white pine, causing small openings and pushing the forest to a climax condition. White pine snags may be smaller in the future and fall down earlier, having effects on those wildlife species that utilize white pine.

Current 1975-era data show zero hectares in M332a with a forest type including white pine. In M333d, about 6 percent of the current hectares have a white pine component in the forest type. Of these, 20 percent are in structure class 3 or 4, 67 percent are in structure class 2, and 13 percent are in structure class 1. Mountain pine beetles will continue to play a critical role in removing the last remnant old growth white pine in the next 40 years. However, until white pine returns as an abundant species component in many forest types, the overall affect of mountain pine beetle in white pine on the forest in general will be relatively minor.

THE ROLE OF DWARF MISTLETOES AS AGENTS AFFECTING SUCCESSION

By Jane Taylor

Dwarf mistletoes are parasitic plants that extract water and nutrients from living conifer trees. The dwarf mistletoes are native components of western coniferous forests, having co-evolved with their hosts for millions of years. The different species of dwarf mistletoes are generally host-specific. Lodgepole pine, Douglas-fir, and larch dwarf mistletoes occur throughout the range of their respective hosts in north Idaho and western Montana (Drummond 1982).

Because dwarf mistletoes are obligate parasites, ecological forces that have patterned the development of the host tree species have also played roles in influencing the distribution of dwarf mistletoes across the landscape. Fire is one of those influential ecological forces. In general, any fire event that kills host tree species will also reduce the population of dwarf mistletoe, at least in the short term. The larger and the more continuous the fire disturbance, the greater the reduction in dwarf mistletoe population at the landscape level. Large, complete burns will greatly reduce dwarf mistletoe populations across the landscape and may even eliminate small, localized populations. Small, "patchy" burns will temporarily reduce segments of dwarf mistletoe populations, but infected residuals provide a ready source of dwarf mistletoe seeds for the infection of the newly developing regeneration (Alexander and Hawksworth 1975).

The parasitic activity of the dwarf mistletoes causes reduced tree diameter and height growth, decreased cone and seed production, and direct tree mortality or predisposition to other pathogens and insects (Hawksworth and Wiens 1996). The effects of dwarf mistletoes on individual trees is generally quite gradual; therefore, the effects of dwarf mistletoes on ecosystem functions will be rather gradual as well. Also, because dwarf mistletoe effects on individuals are generally scattered across a landscape, significant effects on ecosystem functions may only be detectable across a long temporal scale and at the landscape spatial scale.

Table 6.56 shows the percentage of 1975-era sample hectares in M332a and M333d by assigned dwarf mistletoe severity levels for each dwarf mistletoe species. The majority of hectares in both ecosections were assigned severity levels of 0-3. These results indicate that, for the ecosections as a whole, dwarf mistletoes did not play a major role in succession. However, for each dwarf mistletoe species, there were some hectares receiving values of 4-6, indicating that, for some specific polygon classes, dwarf mistletoes may have been an important succession agent. Douglas-fir dwarf mistletoe was identified as the species with the greatest potential for affecting succession with 37 percent and 25 percent of the hectares receiving values of 4-6 for M332a and M333d, respectively. The results also indicate that lodgepole pine dwarf mistletoe was a potentially important agent with 12 percent (M332a) and 16 percent (M333d) of the hectares receiving values of 4-6. Larch dwarf mistletoe appeared to not be a factor at all in M332a, and only a minor factor in M333d.

Table 6.56. Frequency of dwarf mistletoe severity classes assigned to polygons in ecosections M332a and M333d by percent of total 1975-era sample hectares.

Dwarf Mistletoe Severity Class	M332a Percent Hectares by Dwarf Mistletoe Species			M333d Percent Hectares by Dwarf Mistletoe Species		
	Douglas-fir	Larch	Lodgepo-le pine	Douglas-fir	Larch	Lodgepole pine
0	18	82	52	19	45	51
1	28	7	21	43	37	28
2	11	10	12	9	13	4
3	5	0	2	4	0	0
4	21	0	11	20	4	16
5	9	0	0	2	0	0
6	7	0	11	3	0	0

Results of Statistical Analysis of Dwarf Mistletoe APIs and Polygon Characteristics

The statistical analyses consistently found cover type and forest type to be highly associated with dwarf mistletoe probability (Tables 6.57, 6.58, and 6.59). This relationship has biological basis in the host specificity of dwarf mistletoes. Habitat type group was also consistently related to dwarf mistletoe probability. The habitat group association is probably linked to cover type and forest type in that different habitat groups support different tree species. Structure class was also shown to be associated with dwarf mistletoe probability, but to a lesser extent.

Table 6.57. Results of ANOVA using cover type, habitat group, and structure class to predict dwarf mistletoe severity levels.

Dwarf Mistletoe Species	% var.	Factors (most significant to least)
M332a		
Douglas-fir	.75	Cover Type Habitat Group
Larch	.62	Habitat Group Habitat Group*Structure Class Cover Type*Structure Class
Lodgepole Pine	.81	Cover Type

M333d		
Douglas-fir	.58	Cover Type Habitat Group*Cover Type*Structure Class Habitat Group
Larch	.35	Cover Type
Lodgepole Pine	.73	Cover Type Habitat Group*Cover Type

Table 6.58. Results of ANOVA using forest type, habitat group, and structure class to predict dwarf mistletoe severity levels.

Dwarf Mistletoe Species	% var.	Factors (most significant to least)
M332a		
Douglas-fir	.88	forest type forest type*Structure Class Habitat Group*forest type
Larch	.78	forest type Habitat Group*forest type Structure Class
Lodgepole Pine	.83	forest type Habitat Type Habitat Type*forest type
M333d		
Douglas-fir	.76	forest type Habitat Group Habitat Group*forest type
Larch	.71	forest type forest type*Structure Class Structure Class
Lodgepole Pine	.87	forest type Habitat Group*forest type forest type*Structure Class

The finding that cover type was significantly related to dwarf mistletoe probability gives credibility to the method used to calculate API values for the 1935-era data (see Methods section). The results from the statistical analysis provided the guidance for a more detailed

investigation of the association between dwarf mistletoe probability and the three most significant factors: cover type, forest type, and structure class.

Analysis by cover type

An analysis of the association between cover type and dwarf mistletoe API values in M332a and M333d was performed for all three mistletoe species (Table 6.59). As would be expected, the highest API values occurred within the cover types capable of supporting the greatest component of the mistletoe-susceptible species. The cover types with the highest average API values for each species were the same for both M332a and M333d. For Douglas-fir, the highest severity values were in cover types 2,3 and 5. For larch, the value was highest in cover type 3. For lodgepole pine, cover type 7 received the highest value.

Table 6.59. Average dwarf mistletoe severity rating associated with major cover types and the change in percentage of hectares in each cover type between 1935 and 1975 eras.

	Average Dwarf Mistletoe Severity, M332a			Average Dwarf Mistletoe Severity, M333d		
Cover Type	Douglas-fir	Larch	Lodgepole Pine	Douglas-fir	Larch	Lodgepole Pine
1	2.0	1.5	1.5	1.7	1.0	1.0
2.8	0.6	0.1	0	0.9	0	0
2	3.3	0.1	0.3	2.9	0.6	0.6
3	3.0	2.4	0.9	3.3	1.8	0.4
4	NA	NA	NA	1.3	1.0	0.1
5	4.7	0	0.5	3.9	0.3	0.7
6	0.8	0.4	1.4	0.4	0.1	0.5
7	0.7	0.1	4.0	0.8	0.5	3.8
8	1.7	0.6	0.3	1.0	0.7	0.1
9	2.1	0.5	0.4	2.4	1.0	0.5
11	1.8	0.7	1.2	1.3	0.9	0.8
19	1.0	0	0	0.4	0	0.6

Once the important cover types for each dwarf mistletoe species were identified, the 1975-era data were analyzed to determine the percent hectares in the specified cover types with dwarf mistletoe API values of 4-6 (Table 6.60). A comparison between the three dwarf mistletoe species indicates that Douglas-fir and lodgepole dwarf mistletoes are the species with the

greatest potential of causing impacts on succession in both ecosections. Larch dwarf mistletoe received a high API value on a smaller percentage of hectares in the cover type identified as the one where it would the most important, and the average API for larch dwarf mistletoe within that cover type was 2.4 for M332a and 1.8 for M333d.

Table 6.60. Percent of 1975-era hectares in important cover types with dwarf mistletoe API values of 4-6 for each dwarf mistletoe species in M332a and M333d.

Dwarf Mistletoe Species (cover type queried)	Percent 1975-era Hectares	
	M332a	M333d
Douglas-fir (2, 3, 5)	78%	78%
Larch (3)	33%	21%
Lodgepole Pine (7)	93%	91%

Analysis by forest type

Because forest type was identified through the statistical analysis as one of the major factors influencing dwarf mistletoe probability, both ecosections were analyzed by forest type to identify the most important types relative to dwarf mistletoe influence. The 1975-era data were queried to select forest types that were assigned API values 4-6. The forest types selected as being most important relative to potential dwarf mistletoe effects were those with the highest API values that also contained enough hectares to be considered a representative sample (Tables 6.61 and 6.62).

Table 6.61. The five most important forest types for each dwarf mistletoe species based on the average API value and number of hectares represented in the 1975-era data in M332a.

Dwarf Mistletoe Species	Forest Type	1975-era Hectares	Weighted Average API
Douglas-fir	AFDFLP	217.7	4.9
	DF	1,418.3	4.6
	AFDF	139.2	4.5
	AFDFS	102.4	4.3
	DFGFPP	200.3	3.3
Larch	L	14.4	5.0
	DFGFL	60.6	2.8

	AFL S	32.2	2.0
	GFL	4.4	2.0
	AFDFL	69.6	2.0
Lodgepole Pine	LP	539.9	3.6
	AFLPS	416.6	3.1
	DFLP	169.7	2.7
	AFLP	67.0	2.6
	DFGFLP	216.4	2.3

Table 6.62. The five most important forest types for each dwarf mistletoe species based on the average API value and number of hectares represented in the 1975-era data in M333d.

Dwarf Mistletoe Species	Forest Type	1975-era Hectares	Weighted Average API
Douglas-fir	DFL PP	50.9	4.4
	DFL MH	77.2	4.0
	DF	2,292.3	4.0
	DFGF	1,164.2	3.6
	DFGFL	459.7	3.2
Larch	DFL S	56.2	4.0
	GFL	48.0	4.0
	C L WH	109.0	3.8
	DFL WH	132.0	3.8
	L	81.4	3.7
Lodgepole Pine	GFL LP	32.5	4.9
	LPS	83.7	4.3
	LP	1,288.3	4.0
	DFLPPP	157.7	3.9
	AFL LP	85.7	3.9

Douglas-fir dwarf mistletoe. When the total hectares in M332a and M333d were analyzed by forest type, the percent hectares receiving an API value of 4-6 for Douglas-fir dwarf mistletoe were 37 percent and 25 percent, respectively. These numbers indicate that the potential exists for Douglas-fir dwarf mistletoe to be an important agent in these ecosections in some polygons. When the analysis was performed only on the hectares where Douglas-fir was a component in the forest type, 68 percent (M332a) and 52 percent (M333d) of the hectares received a value of 4-6. The average Douglas-fir dwarf mistletoe API value for the hectares where Douglas-fir was a component of the forest type was 3.61 for M332a and 2.89 for M333d. These results indicate that Douglas-fir dwarf mistletoe was potentially important in forest types where Douglas-fir was a major component.

Lodgepole pine dwarf mistletoe. When analyzed by forest type, 12 percent of the total hectares in M332a and 16 percent of the total hectares in M333d received a lodgepole pine dwarf mistletoe rating of 4-6. However, when the analysis was performed on only those hectares where lodgepole pine was a component in the forest type, 56 percent (M332a) and 52 percent (M333d) of the hectares received a rating of 4-6. The average lodgepole pine dwarf mistletoe API value or hectares where lodgepole pine was a component of the forest type was 3.61 for M332a and 3.23 for M333d. These results indicate that lodgepole dwarf mistletoe was probably not an important agent across either ecosection as a whole, but it was potentially important in forest types where lodgepole pine was a major component.

Larch dwarf mistletoe. Queries of the 1975-era data by forest type in both M332a and M333d identified very few hectares with a larch dwarf mistletoe value of 4-6; only 0.6 percent in M332a and 4 percent in M333d of the total hectares received high ratings. The results for M332a, as reported in table 6.61, show that the forest types with the highest larch dwarf mistletoe API values were quite small in size, and probably only represented one or two polygons. The finding that larch was a potentially important agent for such a low proportion of hectares in M332a and M333d is not surprising given the results of the vegetation analysis that showed the proportion of the larch component in both ecosections had dropped substantially by the 1975 era. As the host tree species declines across an ecosystem, the dwarf mistletoe, and its potential effects, will also decline. When the analysis was performed on only the hectares in which larch was a component of the forest type, the percent hectares with an API value of 4-6 was 19 percent for M332a and 30 percent for M333d. These percentages for the hectares with the host tree species in the forest type are lower for larch than for either Douglas-fir or lodgepole pine dwarf mistletoe. This result indicates that out of three dwarf mistletoe species occurring in these two ecosections, larch is the species least likely to play an important successional role. The average larch dwarf mistletoe API for hectares with larch as a component of the forest type was 2.16 and 2.07 for M332a and M333d, respectively. This average API value is relatively low, especially given that it represents the hectares where larch is a component of the forest type. The results from the forest type analysis for larch dwarf mistletoe suggest, that although there is some indications that there are specific vegetation classes where larch dwarf may be an important agent, its overall importance in M332a and M333d is low.

Analysis by structure class

The relationship between structure class and dwarf mistletoe APIs was analyzed using the cover types identified in the cover type analysis (Table 6.57) as being the most important for

each dwarf mistletoe species. The above statistical analysis found structure class to only be a minor factor in predicting dwarf mistletoe severity, but that analysis included structure class 0, which would not support viable dwarf mistletoe populations. Biologically, it is well established that stand structure greatly affects dwarf mistletoe spread and, thus, the affects the parasite has on its hosts. Therefore, it was decided that a more detailed investigation into the relationship between structure class and dwarf mistletoe severity was warranted.

The results from the structure class analysis show that dwarf mistletoe severity is greatest in classes 3 and 4 (Table 6.63). Generally speaking, this finding shows that the older stands with multi-storied structures have a greater potential for supporting populations of dwarf mistletoes capable of causing significant impacts. The average severity values for classes 1 and 2 were surprisingly high. However, a thorough understanding of what structures occur in 1 and 2 lends insight into why this result is possible. A structure class 1 can be very similar to a 4. Both potentially have scattered overstory trees with some regeneration below; the class 1 would have fewer large overstory trees and more regeneration. If the overstory trees and the regeneration are of the same dwarf mistletoe-susceptible species, the ideal structure exists for proliferation of dwarf mistletoe. The structure class 2 stands with high mistletoe API's most likely evolved from the class 1 situation as described above, but the overstory trees have since died and the regeneration as grown into saplings and poles.

The structure class analysis supports findings from the other analyses that Douglas-fir and lodgepole pine dwarf mistletoes have a greater potential for causing succession effects across M332a and M333d than does larch dwarf mistletoe, as evidenced by their relatively higher API values.

Table 6.63. Average dwarf mistletoe severity by structure class within specified cover types for M332a and M333d.

	Weighted Average of Dwarf Mistletoe API by Species (Cover Type Queried)		
Structure Class	**Douglas-fir (2, 3, 5)**	**Larch (3)**	**Lodgepole Pine (7)**
M332a			
Seedling/Sapling (1)	3.6	0	3.8
Pole-size, moderately to well-stocked (2)	3.8	0	4.0
Large-tree, closed canopy (3)	4.0	2.5	4.0
Large and pole-size trees, open canopy (4)	4.1	2.0	4.1
M333d			
Seedling/Sapling (1)	2.9	2.5	3.8
Pole-size, moderately to well-stocked (2)	3.6	1.6	3.8

Large-tree, closed canopy (3)	4.1	2.0	6.0
Large and pole-size trees, open canopy (4)	4.3	2.1	3.7

Analysis of transitions and successional effects

The action probability indices for each dwarf mistletoe species were reviewed for each polygon class (each habitat group, forest type, and structure class combination) in ecosections M332a and M333d, and values of 4-6 were selected as the level at which dwarf mistletoes would have a likely chance of affecting vegetative transitions. Within the polygon classes that received a 4-6 API value, each transition was evaluated to see if dwarf mistletoes would have had a zero, low, moderate, or high potential for affecting the change that occurred. Dwarf mistletoes were considered a potential agent of change only where the transition received a moderate or high rating.

The successional transitions in M332a and M333d that potentially can be attributed to dwarf mistletoe effects can be categorized in two ways: 1) effects on species composition, and 2) effects on the vegetative structure. When reviewing the actual transitions that occurred between 1935 and 1975 eras, it becomes quite apparent that dwarf mistletoe effects on succession are quite dependent on which tree species is infected and the initial successional position of that species (climax or early seral).

When dwarf mistletoes affect early seral tree species, mortality of large, mature individuals affects both stand structure and species composition: there is a reduction in basal area stocking and canopy cover, and the release and accelerated regeneration of the shade-tolerant/climax species. The decreased reproduction potential of the infected early seral species further increases the rate of succession toward climax. Where seedlings and saplings are growing under a heavily infected overstory, the understory trees are killed at an accelerated rate, increasing the rate of succession toward a climax species composition.

When dwarf mistletoes infect climax tree species (Douglas-fir in this analysis), dwarf mistletoe related mortality of large individuals affects stand structure by reducing both basal area stocking and canopy cover. The resulting effects on species composition depend on the existing species mixture. If the site has a heavy early seral component, the result is an increase in the proportional representation of the early seral components. If early seral species no longer occupy the site, there is no species shift. Susceptible seedlings and saplings growing under a heavily infected overstory often die before reaching cone bearing age, resulting in an eventual reduction in stocking. As the overstory is lost, there are fewer individuals in a condition capable of filling in the canopy gaps.

The above general discussion of dwarf mistletoe succession functions provides a biological background for interpreting the transitions that actually occurred in M332a and M333d between 1935 and 1975 eras relative to each of the three dwarf mistletoe species that were analyzed.

Douglas-fir dwarf mistletoe. Examples of the types of transitions potentially influenced by Douglas-fir dwarf mistletoe in M332a and M333d are shown in Table 6.64. The top five in each ecosection, ranked by of number of hectares affected, are shown. In M332a, for all of the transitions in which Douglas-fir dwarf mistletoe played a potential role, 37 percent of the

hectares maintained an early seral species composition; 35 percent of the hectares transitioned to a climax species composition, while the remaining 28 percent showed no change in species composition. In M333d, 68 percent of the hectares transitioned to a climax species composition, 19 percent had no change in species composition, 8 percent maintained the same proportion of the same early seral species, and 5 percent had an increase in the proportional representation of a different early seral species. The analysis of structural change for both ecosections showed that, for the transitions in which Douglas-fir dwarf mistletoe played a potential role, on 100 percent of the hectares, the result was a prevention of canopy closure.

It is highly expected that root disease was the predominant agent responsible for much of the effects potentially attributed to dwarf mistletoe in this analysis. Douglas-fir beetle and spruce budworm may also have produced similar effects.

Table 6.64. The top five transitions, based on number of hectares affected, potentially influenced by Douglas-fir dwarf mistletoe in ecosections M332a and M333d.

Habitat Group	'35-era Forest Type	'35-era Structure Class	'75-era Forest Type	'75-era Structure Class	Cover Change *	Structure Change **	# Hectares
M332a							
2	DF	4	DF	4	none	PC	59
5	DF	4	DF	4	MS	PC	27
1	DFPP	3	DFPP	4	none	PC	25
1	DF	4	DF	4	none	PC	21
1	DF	4	DFPP	4	MS	PC	16
M333d							
4	DFGF	4	DFGF	4	none	PC	44
5	DF	4	GFWH	4	CC	PC	41
5	DFGF	4	GFWH	4	CC	PC	40
2	DF	4	DF	4	none	PC	34
2	DF	2	DF	4	none	PC	31

* cover change: CC = change to climax composition
MS = maintain same early seral components

**structure change: PC = prevent canopy closure

Lodgepole pine dwarf mistletoe. The top five transitions (by number of hectares affected) in M332a for which lodgepole pine dwarf mistletoe had a high potential for affecting the change, are listed in Table 6.65. For the entire M332a ecosection, for those transitions

where lodgepole pine dwarf mistletoe had a high probability of effect, 97 percent of the hectares transitioned toward a climax composition. The remaining three percent maintained an early seral species composition. In M333d, lodgepole pine dwarf mistletoe was identified as a potential agent of change for only six transitions, a total of 88 hectares. In five of the transitions (53 percent of the hectares), the effect on cover was a loss of the lodgepole pine; in the other transition (47 percent of the hectares), the lodgepole pine component was maintained. All six transitions ended in structural class 4, which means that the predominant effect was a prevention of canopy closure. Mountain pine beetle could potentially have had some of the same effects as identified as potential dwarf mistletoe effects.

Table 6.65. The top five transitions, based on number of hectares affected, potentially influenced by lodgepole pine dwarf mistletoe in ecosections M332a and M333d.

Habitat Group	'35-era Forest Type	'35-era Structure Class	'75-era Forest Type	'75-era Structure Class	Cover Change*	Structure Change**	# Hectares
9	LP	4	AFS	4	CC	PC	15
2	LP	4	DF	4	CC	PC	14
2	DFLP	4	DF	4	CC	PC	13
7	LP	4	DFLPPP	4	CC	PC	12
2	LP	4	DFLP	4	CC	PC	7

*cover change: CC = change to climax composition
**structure change: PC = prevent canopy closure

Larch dwarf mistletoe. The top five transitions (by number of hectares affected) in M333d in which larch dwarf mistletoe was identified as playing a potential role are listed in Table 6.66. In the entire M333d ecosection, for the transitions where larch dwarf mistletoe had a potential effect, 90 percent of the hectares transitioned toward a climax composition. On the remaining 10 percent of the area, there was an increase in the proportion of early seral species other than western larch. The analysis of structural change showed that for 100 percent of the area where larch dwarf mistletoe was identified as a potential transition agent, the result was a reduction in basal area stocking and a prevention of canopy closure. In M332a, larch dwarf mistletoe was identified as a potential transition agent on only 155 hectares. Ninety-seven percent of these hectares transitioned to a climax composition, while the remaining three percent showed an increase in the proportion of early seral species other than western larch. The prevailing effect on structure was a prevention of canopy closure.

Dwarf mistletoe is the only significant insect or pathogen that parasitizes or kills western larch. The other agents discussed in the analysis (such as root disease, blister rust, and bark beetles) would actually serve to favor larch in a species mix because of the reduction in competition from other species susceptible to these other agents. It appears highly likely, therefore, that dwarf mistletoe played a very significant role in the transitions that occurred where western larch was a component in the 1935-era forest type.

Table 6.66. The top five transitions, chosen by number of hectares affected, potentially influenced by larch dwarf mistletoe in ecosections M332a and M333d.

Habitat Group	'35-era Forest Type	'35-era Structure Class	'75-era Forest Type	'75-era Structure Class	Cover Change*	Structure Change**	# Hectares
4	DFL	2	DF	4	CC	PC	31
2	DFL	4	DF	4	CC	PC	28
2	DFL	2	DF	4	CC	PC	23
4	DFL	2	DFGF	4	CC	PC	21
4	DFGFL	4	DFGF	4	CC	PC	16

*cover change: CC = change to climax composition
**structure change: PC = prevent canopy closure

Succession Trends in the Subsample of Polygons that Occurred in Both 1935 and 1975 Eras

An analysis was performed to look at the temporal trends in potential dwarf mistletoe effects for the polygons that occurred in both the 1935-era and 1975-era data and then projected into the future to the year 2015 (see the Methods section for an explanation of how the projection was done). Table 6.67 shows the changes over time in the percent hectares in each ecosection with an API value of 4 or greater for each of the dwarf mistletoe species, and Table 6.68 shows the temporal trends in the average dwarf mistletoe API values in both ecosections.

Douglas-fir dwarf mistletoe. In M332a, the percent hectares with a Douglas-fir dwarf mistletoe API of 4 or greater increased between 1935 and 1975 eras, and then was projected to decrease slightly between 1975 and 2015 (Table 6.67). In M333d, the trend was similar, but with smaller increments. In both ecosections, the average Douglas-fir API increased substantially between 1935 and 1975 eras and then increased gradually between 1975 and 2015 (Table 6.67). The increases in both the average Douglas-fir API values and the percent hectares in the higher API classes reflect the vegetation changes that occurred. In both ecosections, the proportion of the Douglas-fir cover type increased substantially between 1935 and 1975 eras (Tables 5.7 and 5.21). Also, there was a general increase in the proportion of the area represented by the older structure classes (Table 5.4 and 5.22). Both of these vegetation changes result in conditions conducive to an increase in dwarf mistletoe effects. Although the proportion of Douglas-fir cover type in both ecosections decreased between 1975 and 2015 (largely due to root disease effects), the proportion of structure class 4 increased, helping to maintain high Douglas-fir dwarf mistletoe API values.

Table 6.67. Percent hectares in M332a and M333d with a dwarf mistletoe API 4-6 for the 1935 era, the 1975 era, and 2015.

Dwarf Mistletoe Species	M332a % Hectares with Dwarf Mistletoe API >4			M333d % Hectares with Dwarf Mistletoe API >4		
	1935	1975	2015	1935	1975	2015
Douglas-fir	22	35	35	24	25	22
Lodgepole Pine	19	14	10	13	16	12
Larch	2	0.7	0.7	6	4	4

Lodgepole pine dwarf mistletoe. In M332a, the percent hectares with a lodgepole dwarf mistletoe API value greater than 3 decreased at each time step (Table 6.67), likely reflecting the decrease in the lodgepole cover type that also occurred (Table 5.7). In M333d, the percent area with a lodgepole pine dwarf mistletoe API value greater than 3 increased between 1935 and 1975 eras and then decreased between 1975 and 2015; the lodgepole pine cover type in M333d followed the same temporal pattern (Table 5.21). The average lodgepole pine dwarf mistletoe API increased slightly in both ecosections between 1935 and 1975 eras and then leveled off between 1975 and 2015. This trend likely reflects the general increase in the proportion of the older structure classes over time (Table 5.22). The aging of the lodgepole component is evidenced by the dramatic loss of the structure class 1 component within the lodgepole cover type. In M332a, the proportion of the lodgepole pine cover type in structure class 1 was 22 percent, 8 percent, and 0 percent in the 1935 era, 1975 era, and 2015, respectively. In M333d, the proportion of the lodgepole pine cover type in structure class 1 was 63 percent, 17 percent, and 18 percent in the 1935 era, 1975 era, and 2015, respectively.

Table 6.68. Weighted average dwarf mistletoe API values for M332a and M333d in the 1935 era, 1975 era, and 2015.

	Weighted Average API Value					
Dwarf Mistletoe Species (cover type queried)	M332a			M333d		
	1935	1975	2015	1935	1975	2015
Douglas-fir (2, 3, 5)	3.0	4.1	4.2	2.8	3.6	4.0
Lodgepole Pine (7)	3.5	3.9	3.9	3.5	3.8	3.7
Larch (3)	1.1	1.4	1.9	2.0	0.9	0.9

Larch dwarf mistletoe. For both ecosections, the percent hectares with a larch dwarf mistletoe API greater than 3 decreased between 1935 and 1975 eras, and then remained constant

between 1975 and 2015. This trend matches the vegetation trends in both ecosections where the larch cover type decreased dramatically over time (Table 5.7 and 5.21). In M332a, the average larch dwarf mistletoe API increased slightly with each time step (Table 6.68). This trend reflects an aging of the larch component in M332a. In the 1935 era, 20 percent of the larch cover type was in structure class 4; by 2015, 55 percent of the larch cover type will be in structure class 4. In M333d, however, there was a slight decrease in the average larch dwarf mistletoe API between 1935 and 1975 eras, and no change between 1975 and 2015. This trend can be explained by looking at the changes in the structure classes that occurred within the larch cover type in M333d. In the 1935 era, 33 percent of the larch cover type was in structure class 4; by the 1975 era, this had dropped to 13 percent, and was projected to remain at 13 percent through 2015.

STEM DECAY FUNCTIONS

By I. Blakey Lockman

Succession Functions

The main function of heartwood in a live tree is to give it vertical stability. The decay of heartwood weakens this vertical stability, making the tree more susceptible to stem breakage. The greater the amount of decay in the heartwood, the more susceptible a tree is to stem breakage.

The main succession function of stem decays are to move stands from a mature closed canopy (structure class 3) to a more open canopy (structure class 4) and to perpetuate such an open canopy (Tables 6.69 and 6.70). This function occurs because stem decays weaken the vertical stability of individual trees, predisposing them to stem breakage which leads to mortality and the formation of small-scale canopy gaps.

In a stand with mixed species, stem decays will occasionally selectively remove the susceptible species and cause a change in species composition. This action constitutes a very minor succession function. An example is a stand containing a grand fir seral component and a cedar climax component: as the grand fir ages, stem decays would aid in selectively removing the grand fir, thus contributing to a species shift to the climax species (cedar), which is not susceptible to the same decay agents as grand fir.

Wildlife Functions

Stem decays are important in the creation of wildlife habitat in living trees, hollow live trees, and hollow dead trees. Living trees with heartwood decay can function as snags, but "the portion of the tree suitable for use by snag-dependent wildlife may be smaller than in a snag of the same size" (Bull et al. 1997). Although primary cavity nesters are capable of excavating in sound wood, they selectively excavate in trees and snags with heartwood decay (McClelland 1977). Most primary cavity nesters do not reuse their holes from one year to the next; their previous year's holes are then used by a multitude of secondary cavity nesters, which are dependent on already-created holes for successful reproduction (McClelland 1977, Cunningham et al. 1980). Thus, cavity nesting habitat as a result of heartwood decay is necessary for the successful reproduction of a number of animal species.

Heartwood decay fungi are also necessary for the formation of hollow trees, which are also important habitat for a number of animal species. "A hollow tree is created when heart-rot fungi invade the heartwood of a living tree, and decay progresses to the point that the cylinder of decayed heartwood eventually detaches from the sapwood and slumps downward, leaving a hollow chamber. This particular decay process is dependent on living trees and the only way to obtain a hollow dead tree or log is to start with a living tree hollowed out by decay" (Bull et al. 1997).

Statistics from M332a and M333d

As indicated in the chapter on methods to assign stem decay API values, there are 3 separate stem decay indices: one for *Echinodontium tinctorium* stem decays on subalpine fir, grand fir, western hemlock and mountain hemlock; a second for stem decays in Douglas-fir, ponderosa pine, western larch, alpine larch, whitebark pine and western redcedar (referred to as "other stem

decays); and a third (*Phellinus pini* stem decay) for lodgepole pine, western white pine, and Engelmann spruce. In general, these three stem decay indices will be addressed together unless it is appropriate to talk about one of them specifically.

Table 6.69: Cover type and structure changes caused by stem decays in ecosection M333d.

TRANSITION TYPES (22,003 total hectares in ecosection M333d)			
Cover Change	**Structure Change**	**Percent of Total Hectares**	**Percent of Transition Type Hectares with High Stem Decay Probability**
No change in cover type	Stand closure prevented (low canopy density results)	1.0	56.6
Increase climax components	Stand closure prevented (low canopy density results)	13.0	4.9
Increase relative proportion of early seral components	Largest trees die: move toward young, small tree classes	2.0	10.4
No change in cover type	Structure stable (no change)	<1.0	64.7
Increase relative proportion of early seral components	Stand closure prevented (low canopy density results)	<1.0	6.3
Increase climax components	Structure stable (no change)	3.0	0.5

Table 6.70: Cover type and structure changes caused by stem decays in ecosection M332a.

TRANSITION TYPES (6,318 total hectares in ecosection M332a)			
Cover Change	**Structure Change**	**Percent of Total Hectares**	**Percent of Transition Type Hectares with High Stem Decay Probability**
Maintain early seral components	Large-tree structure: decrease in canopy density	2.0	65.2
No change in cover type	Stand closure prevented (low canopy density results)	2.0	60..8
Maintain early seral components	Stand closure prevented (low canopy density results)	5.0	12.9
Increase climax components	Stand closure prevented (low canopy density results)	18.0	1.4
Maintain early seral components	Largest trees die: move toward young, small tree classes	5.0	3.4

High stem decay API values are defined as an API of 3 for other stem decay and *P. pini* stem decay, and values of 7 to 11 for *E. tinctorium* stem decay. These high API values were found on 1.7 percent of the entire area in ecosection M333d and 4.2 percent of the area in ecosection M332a in various habitat groups, various forest types, and several structure classes. In ecosection M332a, there are high API values in habitat groups 1, 2, 3, 5, 7, and 9. In ecosection M333d, there are high API values in habitat groups 2, 4, 5, 7, and 9. Ecosection M332a has high API values for all stem decays, while M333d has high API values for *E. tinctorium* stem decay and other stem decay and none for *P. pini* stem decay.

The 1935-era polygon classes with high stem decay API values are dominated by a function in which canopy closure is prevented (PC). In fact, 82 percent of the hectares with high stem decay API values in M333d (Table 6.71) and 65 percent of the hectares with high stem decay API values in M332a resulted in this outcome (Table 6.72). When all the hectares in each ecosection are analyzed, 17 percent of all the functions in M333d and 25 percent of all the functions in M332a were to prevent canopy closure, so it is a significant type of function for both ecosections; and stem decays are one of the significant agents preventing canopy closure. These statistics greatly support the function of stem decays moving stands to a more open canopy and/or perpetuating such an open canopy.

Table 6.71: Cover type and structure changes associated with the highest levels of stem decay API in ecosection M333d.

TRANSITION TYPES RESULTING FROM HIGH STEM DECAY INFLUENCE High stem decay influence was found on 330 hectares in ecosection M333d		
Cover Change	**Structure Change**	**Percentage of High Stem Decay Influence Hectares**
No change in cover type	Stand closure prevented (low canopy density results)	43.6
Increase climax components	Stand closure prevented (low canopy density results)	37.6
Increase relative proportion of early seral components	Largest trees die: move toward young, small tree classes	10.0
No change in cover type	Structure stable (no change)	6.7
Increase relative proportion of early seral components	Stand closure prevented (low canopy density results)	1.2
Increase climax components	Structure stable (no change)	0.9

Table 6.72: Cover type and structure changes associated with the highest levels of stem decay API in M332a.

TRANSITION TYPES RESULTING FROM HIGH STEM DECAY INFLUENCE High stem decay influence was found on 148 hectares in ecosection M332a.		
Cover Change	**Structure Change**	**Percent of Hectares w/High Stem Decay Influence**
No change in cover type	Stand closure prevented (low canopy density results)	39.9
Maintain early seral components	Large-tree structure: decrease in canopy density	30.4
Maintain early seral components	Stand closure prevented (low canopy density results)	17.6
Increase climax components	Stand closure prevented (low canopy density results)	7.4
Maintain early seral components	Largest trees die: move toward young, small tree classes	4.7

Very few of the hectares in both ecosections with high stem decay API values resulted in a change in species composition. Some of these hectares resulted in an increase in the climax species and the remaining hectares resulted in an increase in different early seral components. One example of the latter is a mature open canopy ponderosa pine polygon class changing to a mature open canopy Douglas-fir/ponderosa pine polygon class. The hectares resulting in this change also have high API values for bark beetles in ponderosa pine: although stem decays may have contributed to the loss of ponderosa pine in the overstory, bark beetles were the significant agents causing this change in species composition. Another example is a mature open canopy Douglas-fir/grand fir/western hemlock polygon class changing to a mature open canopy larch/spruce polygon class. Although the hectares in this polygon class have high stem decay API values, they also have high API values for root disease and Douglas-fir bark beetles: both of these agents are much more significant than stem decays in causing the change in species composition on these hectares. Hectares with high stem decay API values resulting in an increase in different early seral components occur only in ecosection M333d, while both ecosections have hectares with high stem decay API values resulting in an increase in the climax species.

An unusual high stem decay function also dominates in M332a and M333d. This function is to prevent canopy closure without changing the cover type. This is an uncommon function in both M333d and M332a (just 1 percent of all hectares in M333d and 2 percent of all hectares in M332a), but is significantly dominated by high stem decay: 57 percent and 61 percent of the hectares with this function have high stem decay API values in M333d and M332a, respectively. **No other agent is predominant in this function**. These statistics support the hypothesis that stem decays have little effect on species composition, but are significant in causing a break-up of the canopy.

Another uncommon, but important, stem decay function in M333d results in maintenance of open canopy conditions (by continual loss of canopy) without causing a change in cover type. This function is seen in habitat group 9, and is limited to the high-elevation types where canopy closure normally does not occur. This function is also uncommon for M333d (less than 1 percent of all hectares). Only 6.7 percent of the hectares with high stem decay influence have this function, but 64.7 percent of the hectares with this function have high stem decay influence. Although it appears stem decays are the main agent in maintaining an open canopy on these hectares, these high elevation sites naturally stay open and canopy closure is rarely achieved.

Another dominant stem decay function in M332a is maintenance of the same early seral components while decreasing the stand density. Greater than 30 percent of all the hectares with high stem decay influence resulted in this function. Sixty-five percent of the total hectares on which the early seral component was maintained and the density was decreased was associated with high stem decay influence. This again displays the function of stem decays having a minor role influence on species composition (in this case, maintaining early seral components), while playing a more significant role in moving stands to an open canopy condition.

Trends and Ecological Implications

There are a number of 1975-era polygon classes in both ecosections with high stem decay API values where no corresponding 1935-era polygon classes exist. These high API values are dominated by stem decay caused by *E. tinctorium*. This implies that *E. tinctorium* is a much more prevalent stem decay now than 40 years ago. The hectares with high stem decay influence from stem decay caused by *E. tinctorium* have increased from 6.5 percent and 5.8 percent to 15.3 percent and 15.5 percent in M333d and M332a, respectively (Tables 6.73 and 6.74). The most apparent explanation for this increase in stem decay caused by *E. tinctorium* is fire exclusion, which has allowed for an increase in the host species. Cover type trends (see Results Part 1, Tables 5.7 and 5.21) indicate there has been a significant increase in the cover types that contain significant components of grand fir, subalpine fir, and western hemlock, hosts for *E. tinctorium*. These cover types are coded as 4, 9, and 11. The combination of these cover types in M332a has increased from 16.4 percent in the 1935 era to 41.1 percent in the 1975 era, and are projected to increase to 44.8 percent by the year 2015. This trend is very similar in M333d, where these cover types have increased from 11.4 percent to 48.8 percent, and are projected to increase to 56.1 percent. Fire suppression has also allowed for the potential buildup of multiple-storied true fir stands. Because of the nature of the infection cycle of *E. tinctorium*, these multiple-storied stands are at a very high "risk" for *E. tinctorium* stem decay infection.

The API values for the other two stem decays changed very little over the last 40 years. The values for M333d increased slightly for both, while the values for M332a decreased slightly for both (Tables 6.73 and 6.74). This implies that, over time and exclusive of management, these two stem decays remain relatively stable as trees and stands age. Although stem decay caused by *P. pini* and stem decay caused by other decay fungi appear to have been relatively stable over the last 40 years, the tree species of most importance to cavity nesters, western larch and ponderosa pine, apparently have decreased. Tables 5.7 and 5.21 (Results, Part 1) display the cover changes that have occurred in the sample over the last 40 years.

Table 6.73: Changes in probable successional importance of stem decay from 1935 to 1975 eras in ecosection M333d.

PERCENT OF HECTARES IN M333D WITH HIGH STEM DECAY INFLUENCE Change over 40 years for each decay type		
Decay Type	**Percent of 1935-era hectares***	**Percent of 1975-era hectares**
Echinodontium tinctorium	6.5	15.3
Phellinus pini	0.4	0.6
Other	0.2	0.3
All Decays	7.0	16.2

*Percentages calculated by applying 1975-era proportions by cover type to 1935-era hectares

Table 6.74: Changes in probable successional importance of stem decay from 1935 to 1975-eras in ecosection M332a.

PERCENT OF HECTARES IN M332A WITH HIGH STEM DECAY INFLUENCE Change over 40 years for each decay type		
Decay Type	**Percent of 1935-era hectares***	**Percent of 1975-era hectares**
Echinodontium tinctorium	5.8	15.5
Phellinus pini	0.8	0.6
Other	1.5	1.2
All Decays	8.0	17.4

*Percentages calculated by applying 1975-era proportions by cover type to 1935-era hectares.

There has been a decrease in percent cover of the three cover types that contain significant components of ponderosa pine and western larch. These cover types are coded as 2.8, 2, and 3. cover type 2.8 (ponderosa pine greater than or equal to 80 percent of the cubic foot volume) has decreased from 3.3 percent to 1.5 percent and 1.3 percent to 0.7 percent in M332a and M333d, respectively, and is projected to continue to decline over the next 40 years to 1.3 percent and 0.6 percent. cover type 2 (ponderosa pine greater than or equal to 25 percent of the cubic foot volume) has decreased from 4.2 percent to 3.0 percent in M333d and is projected to decrease to 2.0 percent by the year 2015. cover type 2 has increased from 7.0 percent to 8.1 percent in M332a, and is projected to continue to increase to 10.9 percent over the next 40 years. This increase in cover type 2 in M332a is likely due to an increase in Douglas-fir from fire suppression which has pushed cover type 2.8 stands into cover type 2 stands. This change can still be interpreted as an overall decrease in ponderosa pine cover. cover type 3 (western larch and Douglas-fir greater than or equal to 75 percent of the cubic foot volume with larch greater than or

equal to 10 percent of the cubic foot volume) has decreased from 10.0 percent in the 1935 era to 0.7 percent in the 1975 era and is projected to decrease to 0.4 percent in M332a. This cover type has significantly decreased in M333d from 16.3 percent to 2.8 percent, and is also projected to decrease to 1.9 percent over the next 40 years. This again is likely due to fire suppression which has allowed the buildup of Douglas-fir, so stands in cover type 3 in the 1935 era moved into other cover types, such as cover type 5 (Douglas-fir greater than or equal to 60 percent of the cubic foot volume), in the 1975 era, and the trend continues into the year 2015. In summary, although the incidence of high probabilities for stem decay caused by other decay fungi and those for decay caused by Phellinus pini have remained stable over the last 40 years, the tree species of most importance to cavity nesting species has decreased, and are projected to continue to decrease over the next 40 years. Other tree species are used by wildlife and are locally very important, but overall, western larch and ponderosa pine are considered to be the most valuable with regards to long-standing cavity nesting habitat (McClelland 1977). The 40-year trend in this analysis has been a decrease in preferred cavity nesting habitat, and this trend is projected to continue over the subsequent 40 years to the year 2015.

SPRUCE BEETLE SUCCESSION FUNCTIONS

By Sandra Kegley

The spruce beetle is a native insect that infests all species of spruce. In the Northern Region, Engelmann spruce is its most common host. Most outbreaks occur following a population build-up in large diameter wind-thrown spruce. Standing trees most susceptible to attack are mature, large-diameter (greater than 16 inches), growing in dense stands with a large component of spruce, and have a slower than average growth rate in recent years. Spruce beetles attack and kill the largest spruce trees in a stand. The spruce beetle is a recycling agent, killing old spruce trees, creating openings that allow younger trees to grow.

Since spruce is seral on all habitat types, the most common affect of spruce beetle killing spruce trees would be to accelerate succession toward a climax forest condition. On spruce forest types, spruce beetles would be responsible for a change in dominant forest type. When large groups of spruce are killed, it may also change forest structure to a younger stage. On forest types other than spruce, spruce beetle would create openings in the forest canopy, changing forest structure. In mixed species, early seral stands, spruce beetle actions may maintain the other early seral species (Figure 6.69). Spruce beetles reduce stand average and maximum tree diameters, heights, and ages; and reduce the spruce component and lower stand density.

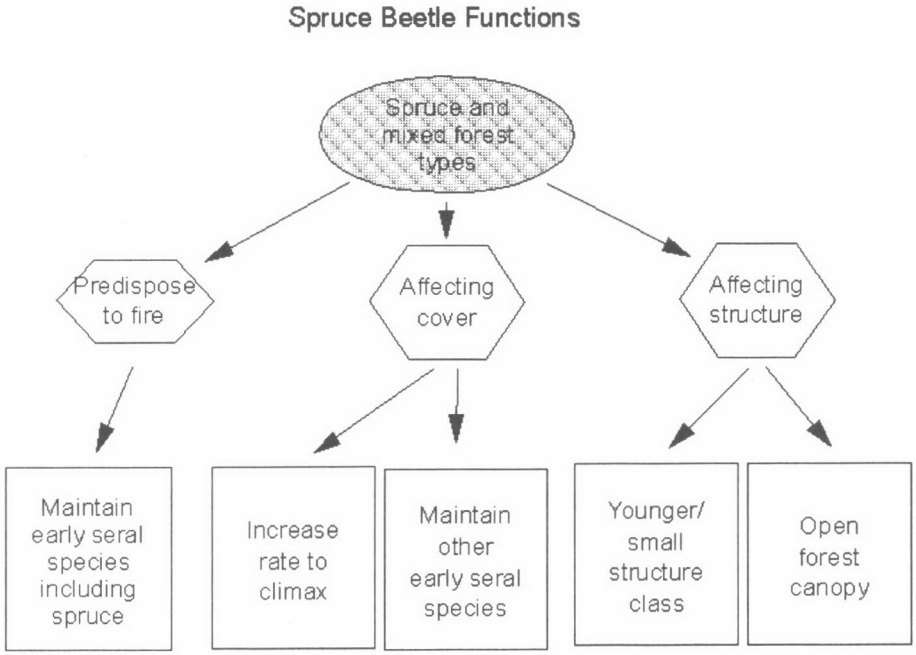

Figure 6.69: Spruce beetle functions.

Most often, spruce beetle will have an affect on mature forests in a closed canopy condition (structure class 3). In this structure class, spruce beetle most likely would accelerate the forest towards a more open, mature structure class (class 4). When very large groups of spruce are killed, the stand may be open enough to change to a younger seedling, sapling, or pole-sized

structure class (classes 1 and 2). In the absence of fire, the response would be an accelerated growth of previously suppressed small diameter trees (Veblen et al. 1991).

Spruce beetles may also have a lesser affect on pole-sized stands (structure class 2) and open canopy pole-sized or mature stands (structure class 4). Changes from structure class 2 to 4 or 2 to 1 could be explained in part by spruce beetle activity. They could also keep a forest in structure class 4 for a longer than normal period of time or cause a change from structure class 4 to a 1 or 2.

Mortality caused by spruce beetles could also predispose a forest to fire, resetting succession and allowing new seedlings to become established. Stand replacing fires favor dominance by spruce or lodgepole, maintaining early seral species. Spruce beetle outbreaks usually shift dominance towards subalpine fir or other shade-tolerant tree species (Veblen et al. 1991).

Statistics from M332a

Most API values for spruce beetle were moderate in ecosection M332a. Two classes in habitat type group 7 had high API values. These were in structure class 3, subalpine fir/Engelmann spruce forest types (47 percent high, 53 percent moderate) and Engelmann spruce (100 percent high). Moderate values occurred in habitat type groups 3, 4, 5, 6, 7, 9, and 10 (moderately warm and moderately dry to cold and moderately dry); subalpine fir, cedar, Douglas-fir, grand fir, larch, lodgepole pine, mountain hemlock, spruce and whitebark pine forest types (and combinations of these species); and in structure classes 2, 3, and 4. The majority of moderate API values occurred in structure class 3.

Many habitat type/forest type/structure class combinations, where moderate or high spruce beetle API values occurred, did not exist in our 1935-era database, so many transitions could not be analyzed. One transition seen in M332a had high probability of being caused by spruce beetle. In this a subalpine fir/spruce forest type, structure class 3, habitat type group 7 changed to mountain hemlock forest type, structure class 3. With a high spruce beetle API value, this transition was considered to have high probability of having been caused by spruce beetle activity. The result was an acceleration to climax forest type. Other transitions occurred in a variety of forest types with a spruce component in structure class 3, habitat type groups 3 and 7. The majority of these transitioned to a climax forest type, structure class 3, with the loss of spruce (78 percent). The remainder became mixed forest types with younger structure classes (22 percent). These transitions were considered to have a moderate probability of having been caused by spruce beetle activity (Figure 6.70).

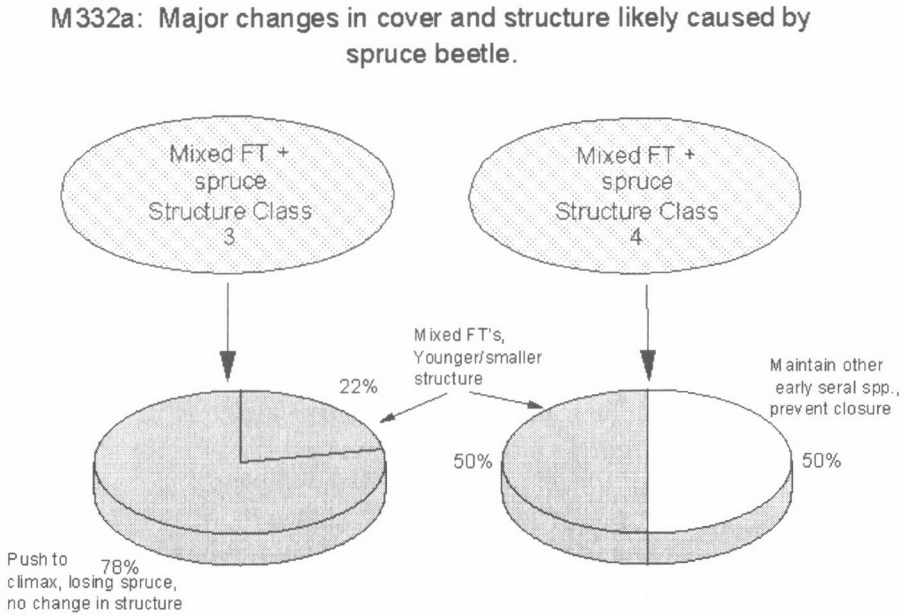
M332a: Major changes in cover and structure likely caused by spruce beetle.
Mixed FT + spruce Structure Class 3
Mixed FT + spruce Structure Class 4
Mixed FT's, Younger/smaller structure
22%
Maintain other early seral spp., prevent closure
50%
50%
Push to climax, losing spruce, no change in structure
78%

Figure 6.70: Major changes in cover and structure likely caused by spruce beetle in mixed spruce stands, M332a.

In habitat type group 9, mixed forest types with a spruce component, structure class 4, transitioned to mixed forest type, structure class 2 (earlier structure class) (50 percent); and other early seral forest type (with the loss of spruce), structure class 4 (50 percent). These transitions were given a moderate probability of occurring due to spruce beetle activity (Figure 6.79).

Statistics from M333d

Only moderate spruce beetle API values occurred in ecosection M333d. These occurred in habitat type groups 4, 5, 7, 9, and 10 (moderately warm and moist to cold and moderately dry); subalpine fir, cedar, Douglas-fir, grand fir, larch, lodgepole pine, mountain hemlock, spruce western white pine and whitebark pine forest types, and various combinations of these forest types; and structure classes 2, 3, and 4. The majority occurred in structure class 3.

Many polygon classes where moderate spruce beetle API values occurred did not occur in the 1935-era database so many transitions could not be analyzed. In fact, there were no classes in structure class 3 that had moderate spruce beetle APIs (where the majority of spruce beetle occurred) in the 1935-era data. Transitions that occurred in this ecosection that could have been attributed to spruce beetle occurred in habitat types 7 and 9 and structure classes 2 and 4.

The following transitions were assigned a moderate probability of occurring due to spruce beetle activity. In mixed forest types with a spruce component, structure class 2, 83 percent stayed the same forest type but changed to structure class 4; 17 percent transitioned to a climax forest type, structure class 1, with the loss of the spruce component (Figure 6.71). In mixed forest types with a spruce component, structure class 4, 44 percent stayed the same forest type but changed to structure class 2 (earlier structure class); 48 percent transitioned to a climax forest

type without spruce, structure class 1 (earlier structure class); and 8 percent transitioned to a climax forest type without spruce, structure class 3 (Figure 6.71). In climax forest types, structure class 4, 30 percent transitioned to climax forest type, structure class 2 (earlier structure class); and 70 percent stayed climax forest type, structure class 4 (maintaining open canopy). In spruce forest types, structure class 2, 100 percent transitioned to non-forest. However, this occurred on very small acreage. In spruce forest type, structure class 4, 26 percent transitioned to climax forest type with spruce, structure class 2 (increase climax components and change to younger structure class); and 74 percent transitioned to climax forest type (loss of spruce component), structure class 3 (Figure 6.72).

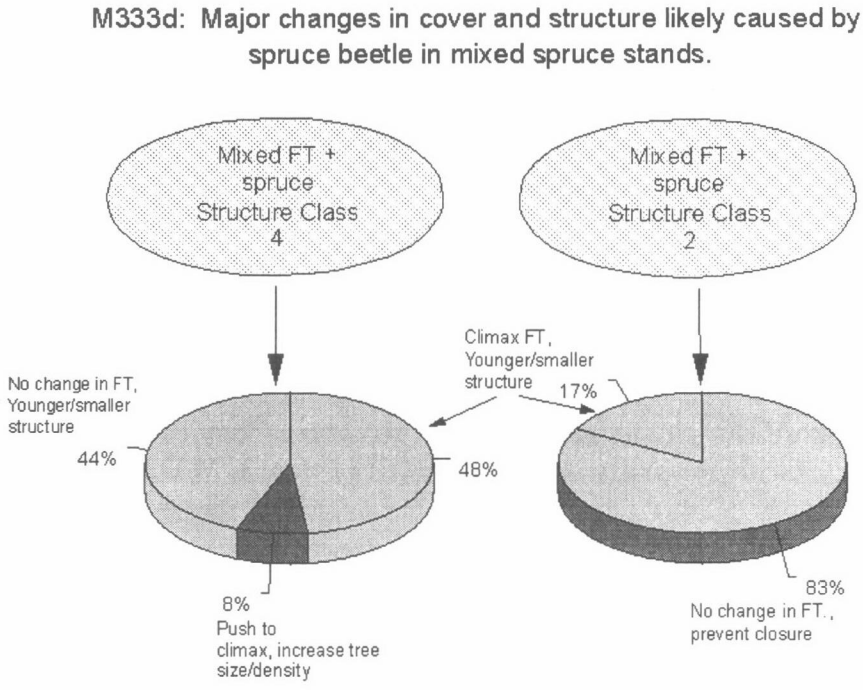
M333d: Major changes in cover and structure likely caused by spruce beetle in mixed spruce stands.
Mixed FT + spruce Structure Class 4
Mixed FT + spruce Structure Class 2
Climax FT, Younger/smaller structure
17%
No change in FT, Younger/smaller structure
44%
48%
8%
Push to climax, increase tree size/density
83%
No change in FT., prevent closure

Figure 6.71: Major changes in cover and structure likely caused by spruce beetle in mixed spruce stands, M333d.

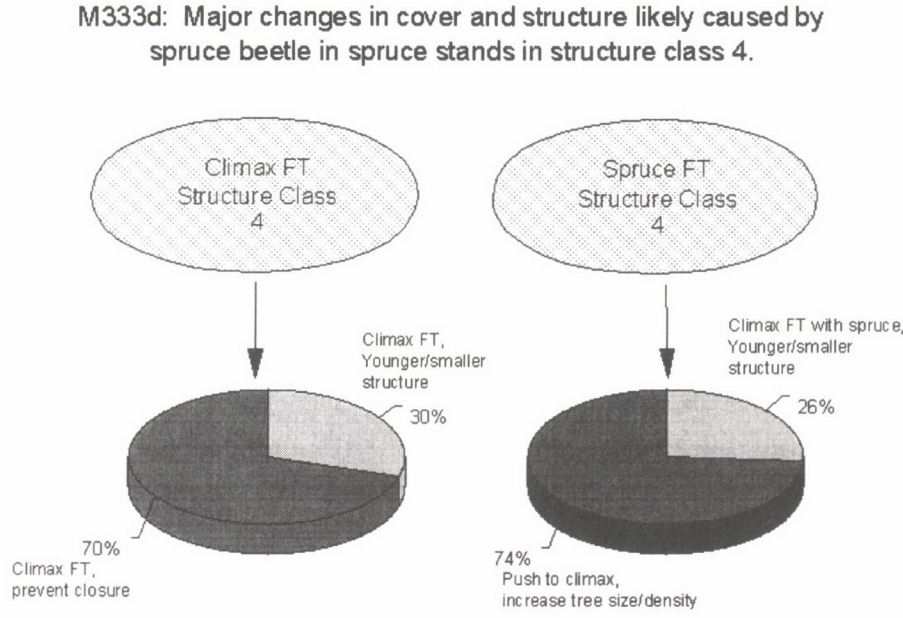
M333d: Major changes in cover and structure likely caused by spruce beetle in spruce stands in structure class 4.
Climax FT Structure Class 4
Spruce FT Structure Class 4
Climax FT, Younger/smaller structure
30%
70%
Climax FT, prevent closure
Climax FT with spruce, Younger/smaller structure
26%
74%
Push to climax, increase tree size/density

Figure 6.72: Major changes in cover and structure likely caused by spruce beetle in spruce stands in structure class 4, M333d.

Overall Status Within the Sample

Transitions occurring in M332a that were attributed to spruce beetle with a high or moderate probability covered 41 hectares or less than 1 percent of the total sample area. Moderate spruce beetle probabilities for causing a change in forest succession in M333d occurred on 400 hectares, or 2 percent of the total sample area. There were many habitat type/forest type/structure class combinations in these two ecosections with high or moderate spruce beetle API values that we did not have in the 1935-era database, so many polygon classes could not be analyzed for transition types.

Comparisons Between M332a and M333d

Transitions were similar in these two ecosections where we had data to analyze. The majority of the transitions in both ecosections resulted in an acceleration to climax forest type with the loss of the spruce component and a change in structure classes. Changes in structure resulted in a younger structure class most often or to an open forest canopy.

Ecological Implications

Spruce beetle outbreaks have occurred in the past over huge acreages where there are large expanses of spruce. Striking outbreaks have occurred in Colorado, southern Idaho, Alaska, and Canada. Outbreaks have also occurred in parts of the Northern Region on a somewhat smaller scale, but causing significant tree mortality. These outbreaks are usually triggered by

windthrow events, which allow spruce beetle populations to rapidly expand in downed trees and subsequently move to standing trees.

In ecosections M332a and M333d, there are no large expanses of spruce. Spruce occurs in small patches, most often in riparian areas or high elevation stands. Spruce beetle activity in riparian areas will add large woody debris to streams, but also cause a loss of solar insulation. Endemic spruce beetle activity is probably beneficial by slowly adding high quality snags over time. Outbreaks cause the loss of spruce component in a few years time, and a subsequent rapid change in dominate tree species and forest structure. These areas will be dominated by climax species and forest structure will change to younger classes or open canopies, and there will be a loss of large-diameter snags to replace woody debris in streams.

High elevation stands with spruce beetle activity will also transition to climax forest species at a faster than normal rate. Forest types will change from spruce to subalpine fir and mountain hemlock, which may or may not be desirable. These tree species are more susceptible to decay and root disease.

WESTERN SPRUCE BUDWORM SUCCESSIONAL INFLUENCES

By Nancy Sturdevant

Introduction

In the Northern Region, western spruce budworm (*Choristoneura occidentalis*) populations can be found throughout the Idaho panhandle, western and west-central Montana and northwestern Wyoming. Budworm outbreaks are more common and can have larger impacts on forests east of the Continental Divide in west-central Montana as well as the Bitterroot National Forest and portions of the Lolo National Forest in western Montana and Nez Perce National Forest in northern Idaho.

Transition Patterns in M332a

Both the cyclical and persistent transition patterns occurred in ecosection M332a. The persistent pattern is described as occurring consistently in an area and usually causes varying degrees of mortality. The cyclical pattern is described as having a regular cycle (every 20 to 30 years) and causes mortality in smaller size classes of trees. Both patterns can affect succession pathways.

Out of the 4,328 hectares sampled in both 1935 and 1975 eras in M332a, transitions that may have been significantly influenced by budworm occurred on 188 hectares or approximately 4 percent. Seven out of eight transitions on this 188 hectares of M332a are characterized by persistent patterns. The remaining transition is characterized by a cyclical pattern. Examples of persistent population patterns are common east of the Continental Divide in west-central Montana and in limited areas west of the Divide. Parts of the Bitterroot and Nez Perce National Forests display this pattern and are included in M332a. When budworm functions in this manner, it usually causes mortality in sapling and pole-size trees, creating small to moderate openings over time especially on grand fir habitat types.

Transitions in M332a

The transitions that budworm were significant in were found in habitat groups 2 (157 hectares), and 5 (31 hectares). Habitat group 2 is mostly Douglas-fir and grand fir habitat types and is moderately warm and dry. Habitat group 5 is western redcedar and western hemlock habitat types and is moderately moist and wet. Six out of eight of the transitions where budworm had a high probability of effect, where in habitat group 2. Several studies have shown that budworm causes the most damage on warm, dry sites. All of the transitions with moderate and high APIs started as a Douglas-fir forest type in either structure class 2 or 4. They all moved to structure class 4 with the exception of one that remained in structure class 2. In this transition, the Douglas-fir remained, but the proportion of subalpine fir and lodgepole pine in the stand increased. For the transitions that moved to structure class 4, they were primarily Douglas-fir stands. However, 21 hectares went from Douglas-fir forest type/structure class 2 (DF/SC 2) to Douglas-fir/ponderosa pine forest type/structure class 4 (DFPP/SC 4). This is significant relative to the number of hectares with moderate or high budworm probabilities.

Succession Functions of Budworm in M332a

Budworm functions in four ways in M332a:

1) Increasing or maintaining the early seral tree species in stands while preventing canopy closure in mature stands. This is seen in the transitions from DF/SC 4 to DFPP/SC 4 or DFLP/SC 4. For these transitions, budworm may function by killing seedling, sapling, and pole-size trees of host species, thus allowing less competition for larger Douglas-fir and non-host early seral species such as ponderosa pine and lodgepole pine. The larger Douglas-fir may also lose their competitive edge due to dieback further releasing early seral species. These polygons also had high probabilities of Douglas-fir dwarf mistletoe and Douglas-fir stem decay influences as well as moderate root disease and Douglas-fir beetle influences. Twelve hectares underwent these transitions; 6 percent of the hectares with moderate to high budworm probabilities.
2) Preventing canopy closure without altering species composition as seen in DF/SC 4 remaining DF/SC 4. This transition is associated with high budworm APIs in both habitat groups 2 and 5. In this example, mortality may be confined to the smaller size class trees. Budworm also effects regeneration of the stand by impacting seed production. Even in lightly defoliated stands, budworm significantly decreases seed production during an outbreak. Two-thirds of the hectares in these polygons also had high probable influences from Douglas-fir dwarf mistletoe and Douglas-fir stem decay as well as moderate influences from root disease and Douglas-fir beetle. The remaining one third had high root disease and Douglas-fir dwarf mistletoe influence and moderate Douglas-fir beetle probability. Eighty-six hectares, or 46 percent of the hectares with moderate to high budworm influence, underwent this type of transition.
3) Increasing or maintaining early seral species while preventing canopy closure in maturing stands. This is seen in the change from DF 2 to DFLP 4 or DFPP 4. Budworm functions in these transitions by opening up the stand as it moves from SC 2 to SC 4 by causing mortality in smaller size trees. For these transitions, budworm probably plays a significant role in the stand development. These types of stands were warm, dry sites where the most significant budworm damage occurs. As the stand matures, budworm removes pockets of regeneration and pole-size trees, thus allowing early seral component of the stand as well as larger DF to remain in a dominant position as the stand matures. These polygons were also had moderate probable influence from both root disease and Douglas-fir dwarf mistletoe. This type of transition was seen on 29 hectares: 15 percent of the hectares with moderate to high budworm influence.
4) Preventing stand closure in the maturing stand in which the non-host climax species is increasing in composition. This is seen in DF 2 becoming CDF 4. This transition, involving only 4 hectares, occurred on moist, cool sites, budworm probably does not play a significant role in succession. Individual small trees in these types of stands may be killed, allowing an existing cedar in the understory to mature. This stand also had moderate influence from root disease, Douglas-fir beetle and Douglas-fir dwarf mistletoe.

One stand which was a DF 2 on a habitat type group 2 site, had a moderate probability for budworm influence. This stand remained in SC 2 but LP and AF begin to fill in the canopy. Even though this stand received a moderate API value, it is unlikely that budworm played a significant role in this change. This stand also had moderate root disease influence.

of the longer recovery period between outbreaks that is associated with the cyclical pattern. Bousefield et al. (1973) showed an increase in growth of lodgepole pine and ponderosa pine following a budworm outbreak, while all host trees decreased in growth. The study was conducted in area that displayed a cyclical budworm pattern.

Future Trends

Anderson et al. (1987) conducted a study in western Montana examining the relationship between forest fire frequency and western spruce budworm outbreaks. They found that, although the frequency of budworm outbreaks in western Montana had not increased since 1910, the intensity of outbreaks had significantly increased. This is probably due in part to the decrease in fire frequency, which has changed forest vegetation patterns, resulting in increased acreages of multi-storied stands that are excellent budworm habitat (Fellin 1979 and Carlson et al. 1986). This condition is represented in many of the transitions where budworm had a high API value.

In our sample of M332a, the proportion of sample hectares that were in polygon classes expected to have significant budworm influence increased slightly from 4 percent in the 1935 era to 5 percent in the 1975 era. For M333d, the increase was somewhat greater, going from 2 percent in the 1935 era to 4 percent in the 1975 era. Anderson et al. (1987) found that the duration of a budworm outbreak increased from 13.3 years prior to 1910, to 25.4 years after 1910. This trend is likely to continue to remain a common scenario in many areas in the Northern Region This could change if forests that are highly susceptible to budworm and have persistent patterns, are managed with fire or other management practices that emulate pre-1930s conditions.

Summary and Conclusions

The dominant outbreak pattern in M332a is the persistent pattern. In this pattern, budworm functions by retarding succession or keeping stands in a low-density condition. Budworm is very active in these stands but is just one of several succession factors such as root disease, Douglas-fir beetle, and bark beetles in ponderosa pine, that affected transitions in these stands. Stands in M333d display a cyclical pattern of budworm outbreaks. Less mortality and growth loss occur in these stands due to budworm. Therefore, we see more budworm host trees, such as grand fir, remaining in the stands.

The primary difference between M332a and M333d is that budworm is less active in M333d, and does not play as a significant a role in succession as it does in M332a. This conclusion is substantiated in the mostly moderate API values in M333d. Most of the same polygons affected by budworm were also subject to other insects or pathogens: Douglas-fir dwarf mistletoe, Douglas-fir stem decay, root disease or Douglas-fir beetle had moderate to high probable influence on all transitions in polygons which had moderate to high budworm probabilities. Bousefield and Williams (1977) did not find the incident of stem decay to increase following a budworm outbreak; however, several studies have suggested there may be an increase in Douglas-fir beetle following a budworm outbreak.

Transition Patterns in M333d

Out of the 19,563 hectares sampled in both 1935-era and 1975-era surveys in ecosection M333d, 365 hectares had moderate to high probable influence by budworm or approximately 2 percent. The transitions that budworm was significant in were found in habitat groups 2, 4 and 5. Habitat groups 2 and 5 are described in the above paragraph. Habitat group 4 is described as wet grand fir habitat types and moderately warm and moist. The highest budworm hazards occurred on the dry, warm habitat types in group 2. A total of 18 transitions occurred that may have been significantly influenced by budworm. Of these, 12 transitions (287 hectares) had moderate API values and 6 (61 hectares) had high API values. The forest type the majority of the transitions started as were either pure Douglas-fir stands or a combination of Douglas-fir and grand fir and sometimes varying amounts of other species such as larch. The stands started out in structure classes 2 and 4 and all went to structure class 4 by the 1975 era. All transitions had a cyclical pattern with the exception of two that had a limited budworm pattern. The two transitions that are described with a limited pattern only accounted for a total of 18 hectares and were deemed not significant. The most significant transitions occurring in M333d had both high APIs and occurred on more than 10 hectares. The two transitions are: DF/SC 2 to DF/SC 4 (52 hectares) and DF/SC 4 remaining DF/SC 4 (34 hectares). For transitions in M333d, budworm functioned in the same way as in M332a by killing sapling and pole-size trees, thus creating small openings for release of early seral species and by keeping or moving stands in what may be a multi-storied structure. However, because budworm occurred only in a cyclical or limited pattern, damage from budworm over time was less significant than in M332a where budworm generally occurred in a more persistent pattern. Therefore, transitions in M333d, only had moderate APIs, and other agents may have played a more significant role in these transitions.

Transitions in M333d

Previous studies conducted in the Northern Region have shown that very little mortality occurs from budworm even following a significant outbreak. The greatest impact caused by moderate and severe budworm defoliation is growth loss. Bousefield and Franc (1979) showed that growth loss following a budworm outbreak ranged from 1.71 percent to 10.47 percent per acre annually for many years. On the Nez Perce National Forest, which displays a persistent pattern, 19.07 percent mortality occurred in one heavily defoliated area but was confined primarily to the smaller diameter trees (Bousefield and Williams, 1977). This supports many of the transitions in the query where budworm had a high API. As these stands matured from SC 2 to SC 4, budworm was actively removing smaller size trees from the stand, thus allowing larger Douglas-fir and other non-host species to retain their position in the canopy. For those stands with high budworm APIs that remained in SC 4, over a 40-year period, mortality of smaller size trees from budworm defoliation was in part the reason those stand remained in that condition. During a budworm outbreak, some of the sapling and pole-size trees may have been killed outright or damaged to where they would not survive by severe and repeated defoliation. But once the outbreak subsided, the seed-bearing trees probably quickly began to regenerate the stand with small Douglas-fir. Also as shown in M333d, many budworm-impacted stands had larger Douglas-fir and non-host species in structure class 4. This is most likely due to the repeated defoliation and mortality of smaller host trees, and therefore allowing larger host and non-host trees in the stand improved growing conditions. This scenario is more prominent in M333d than M332a because

THE CO-OCCURRENCE OF PATHOGENS AND INSECTS IN SAMPLE POLYGONS: RELATIONSHIPS AMONG APIs

By Michael Marsden

Ninteen unique indices (Table 6.75) were used to associate the successional roles of pathogen and insects with changes in vegetation during the roughly 40 years between 1935-era and 1975-era surveys. Most of the indices rated the relative suitability of stands for specific types of actions by the pathogen or insect. Root disease severity was a more direct assignment of relative degree of observable effect on stands based on photointerpretation. A few other indices examined the ecological role of the host species in the stand as a mean to evaluate the potential effects of insects or pathogens. These were used in combination with the action probability index for a given insect or pathogen.

Some of the indices were regarded as nominal values (Table 6.75): for example root disease severity was assigned as classes 0 through 9, but the scale was considered continuous rather than discrete classes. Other indices were discrete classes (Table 6.75), such as the "high, moderate, low, or none" values used to rate the relative probability of significant action by bark beetles. These were generally calculated as nominal values and then placed into discrete classes based on a range of nominal values.

Table 6.75: Action probability index value types for pathogens and insects included in this analysis.

ACTION PROBABILITY INDICES USED IN THIS ANALYSIS			
Abbreviation	**Index Name**	**Nominal Values**	**Class Values**
DCYET	Stem decay of true firs and hemlocks	X	
DCYLP	Stem decay of lodgepole pine	X	
DCYOT	Stem decay in other tree species	X	
DFBGR	Douglas-fir beetle group attack		X
DFBWD	Douglas-fir beetle weeding		X
DMDF	Douglas-fir dwarf mistletoe	X	
DMLP	Lodgepole pine dwarf mistletoe	X	
DMWL	Western larch dwarf mistletoe	X	
LPROLE	Successional role of lodgepole pine		X
MPBLP	Mountain pine beetle in lodgepole pine		X
MPBPP	Mountain pine beetle in ponderosa pine		X
MPBWBP	Mountain pine beetle in whitebark pine		X
MPBWP	Mountain pine beetle in western white pine		X

PPROLE	Successional role of ponderosa pine		X
RRSV	Root disease severity	X	
SB	Spruce beetle		X
WPBRH	White pine blister rust hazard	X	
WPBRP	White pine blister rust severity	X	
WSBW	Western spruce budworm	X	X

Results of Statistical Tests for Ecosection M332a

Relationships among pairs of APIs are presented first for ecosection M332a (Tables 6.76 through 6.84). This is followed by the appropriate tables for ecosection M333d. For the pairs of nominal valued action probability indices (APIs), a correlation coefficient was computed. This statistic indicates the degree of agreement between the two APIs. Positive values indicate that high values of one API are associated with high values of the other. Negative values indicate that high values of one is associated with low values of the other. The magnitude of the correlation coefficient indicates how strong the association is. Values near 1 indicate a strong relationship; values near zero indicate a weak one.

Table 6.76: Correlation coefficients for ecosection M332a for pathogens and insects with nominal Action Probability Indices.

M332a: Correlation Coefficients for Nominal Indices										
	RR-SV	**WP-BRH**	**WP-BRP**	**DM-DF**	**DM-WL**	**DM-LP**	**WSB-W**	**DCY-ET**	**DCY-LP**	**DCY-OT**
RRSV	+1.0									
WPBRH	+.49	+1.0								
WPBRP	-.01	+.00	+1.0							
DMDF	+.00	-.21	-.01	+1.0						
DMWL	+.22	+.28	-.01	-.10	+1.0					
DMLP	-.14	-.03	-.02	-.26	+.09	+1.0				
WSBW	+.08	+.13	-.01	+.20	+.03	-.18	+1.0			
DCYET	+.18	+.18	+.00	-.34	+.26	+.05	+.02	+1.0		
DCYLP	-.12	-.01	-.01	-.28	-.09	+.78	-.14	-.19	+1.0	
DCYOT	-.20	-.27	-.03	+.55	-.10	-.37	+.09	-.53	-.33	+1.0

The index for root disease severity (RRSV) has it's highest positive correlations (+.49) with those for white pine blister rust hazard (WPBRH) and western larch dwarf mistletoe (DMWL) (+.22). The other positive correlations with RRSV are less than 0.20. The greatest negative correlation of RRSV is -0.20 with stem decays other (DCYOT), which includes decays in tree species other than hemlocks, true firs, and lodgepole pine. The strongest positive correlation in the table is +0.78 for lodgepole dwarf mistletoe (DMLP) and *Phellinus pini* stem decay in lodgepole pine (DCYLP). Both of these APIs may key on the presence of mature lodgepole pine trees in the stand. The square of the coefficient is 0.61, which indicates that 61 percent of the variation in one of the API is associated with variation in the other. The strongest negative correlation is -.53 for *Echinodontium tinctorium* in western hemlock or true firs (DCYET) and DCYOT.

Analysis of variance for combinations of nominal and class-valued indices

When the first API in a pair is nominal valued and the second API indicates only discreet classes, the correlation coefficient can not be calculated. In this case, to test for an association between the two APIs, the nominal valued API is considered to be the dependent variable and the class-valued API is considered to be classes for an analysis of variance. For example, let us take the index for Douglas-fir dwarf mistletoe (DMDF) , and the index for the weeding function of Douglas-fir beetle (DFBWD): the sample data for ecosection M332a is re-stratified by the four classes (0, C, R, and S) for DFBWD and an analysis of variance is computed to test if the average value of DMDF differs for the four classes. Stratification of stands by DFBWD accounts for 52 percent of the variation in DMDF, and the F-test is highly significant. This value is comparable to the square of the simple correlation coefficients used to comparing two nominal valued APIs. So here, we would conclude that DMDF and DFBWD are related APIs.

Table 6.77: Analysis of Variance for a nominal index (Douglas-fir dwarf mistletoe) compared to a class-valued index (Douglas-fir beetle weeding action) in ecosection M332a.

DFBD Class	Mean DMDF API
0	0.8
C	2.7
R	4.9
S	1.5

Source	Degrees freedom	Sum of Squares	Mean Squares	F value	Prob > F
Groups (DF-BWD)	3	14584.95	4861.65	157.96	<0.0001
Within groups	429	13203.49	30.78		

R-squared = 0.525

The nominal API are reported in Table 6.78 by the Class Valued API giving only the R-square from the analyses of variance. The grouping of the DCYLP APIs by MPBLP accounts for the most variation in DCYLP, although it is only 50 percent. This is likely a result of both agent requiring mature lodgepole pine for significant effect. MPBLP classes also account for a significant amount of the variation in DMLP for similar reasons. For the most part, the relationships among the indices appear weak based on R-squared values which are generally less than .20.

Table 6.78: R-squared from the Analyses of variance for nominal APIs, reported by the class-valued API in ecosection M332a.

M332a: R-squared for Nominal-valued Indices by Class-valued Indices.										
Class Valued Indices	**RRSV**	**WP-BRH**	**WP-BRP**	**DMDF**	**DMW-L**	**DM-LP**	**WSB-W**	**DCY-ET**	**DCY-LP**	**DCYO-T**
DFBGR	0.002	0.001	0.000	0.211	0.001	0.015	0.128	0.012	0.032	0.100
MPBLP	0.043	0.034	0.000	0.014	0.014	0.485	0.010	0.021	0.507	0.102
MPBPP	0.067	0.240	0.000	0.038	0.033	0.073	0.023	0.069	0.026	0.141
MP-BWP	0.007	0.002	0.045	0.001	0.035	0.002	0.005	0.002	0.003	0.007
MP-BWBP	0.007	0.002	0.000	0.009	0.009	0.006	0.003	0.012	0.010	0.006
SB	0.056	0.018	0.006	0.043	0.087	0.006	0.001	0.257	0.015	0.077
WSBW	0.116	0.018	.002	0.303	0.014	0.151	0.086	0.079	0.220	0.011

Chi-square tests for APIs that are class-valued variables

The last set of pairs of APIs to examine for ecosection M332a are those in which both APIs are class-valued variables. Here we calculated a Chi-square test from the contingency table

of the frequency of stands. For simplicity, the unweighted frequencies are used in the calculations. For the successional role of lodgepole pine, LPROLE (an index used to evaluate the API for mountain pine beetle) and the API for the weeding function of Douglas-fir beetle, DFBWD, the Chi-square test results are as follows.

Table 6.79 : Chi-square test for Douglas-fir beetle weeding function API by the successional role of lodgepole pine, LPROLE in ecosection M332a.

M332a: Chi-square Test: Douglas-fir Beetle Weeding Function API by the Lodgepole Role					
LPROLE	**0**	**C**	**R**	**S**	**ROW TOTAL**
C	66	47	11	3	127
D	78	50	16	6	150
M	57	68	40	9	174
COLUMN TOTAL	201	168	67	18	451

Chi-square = 23.85 with DF = 6 and significance >0.0056

The significance Chi-square indicates that the patterns are not independent between the two APIs. This can be seen more clearly if we examine the DFBWD values for fixed values of LPROLE. When LPROLE had the value of D, 16 stands (11 percent of the stands in D) fell in the R class for DFBWD. When LPROLE had the value of M, 40 stands (23.0 percent of the stands in M) fell in the R class for DFBWD. The pattern of stands by DFBWD classes changes with different values of LPROLE: the two are not independent APIs.

For the rest of the combinations examined, only the significance level of the test of independence is given. Only combinations that involve different agents are tested.

Table 6.80: Significance level for Chi-square tests comparing class-valued APIs in ecosection M332a.

M332a: Significance Levels from Chi-square Test for class-valued APIs										
	DF-BGR	**DF-BWD**	**MP-BLP**	**LPR-OLE**	**MP-BPP**	**PPRO-LE**	**MP-BWP**	**MP-BWBP**	**SB**	**WSB-W**
MP-BLP	.011	.220								
LPRO-LE	.562	.001								
MPBPP	.013	.000	.047	.006						

PPRO-LE	.382	.000	.000	.000						
MP-BWP	.434	.012	.843	.112	.877	.118				
MP-BWBP	.952	.479	.972	..427	.991	.116	.999			
SB	.656	.000	.009	.000	.066	.000	.493	.005		
WSBW	.000	.000	.000	.005	.000	.000	.883	.823	.001	

Many of the indices can be seen to be dependent. For example, the DFBGR index in Table 6.79 is not independent of MPBLP, MPBPP, or WSBW. The pattern values in DFBGR will change with levels of these APIs.

Results of Statistical Tests for Ecosection M333d

Table 6.81: Correlation coefficients for ecosection M333d for pathogens and insects with nominal Action Probability Indices.

M333d: Correlation Coefficients for Nominal Indices										
	RR-SV	**WP-BRH**	**WP-BRP**	**DM-DF**	**DM-WL**	**DM-LP**	**WSB-W**	**DCY-ET**	**DCY-LP**	**DCY-OT**
RRSV	+1.0									
WP-BRH	-.09	+1.0								
WP-BRP	-.07	+.25	+1.0							
DMDF	+.15	-.12	-.06	+1.0						
DMWL	+.04	+.24	+.06	+.05	+1.0					
DMLP	-.15	-.12	-.02	-.20	-.04	+1.0				
WSBW	+.14	-.03	-.11	+.40	+.03	-.17	+1.0			
DCYET	+.13	+.12	-.03	-.30	-.05	-.25	-.02	+1.0		
DCYLP	-.13	-.02	+.28	-.24	-.05	+.66	-.20	-.32	+1.0	
DCYO-T	+.07	-.14	-.10	+.66	+.18	-.27	+.25	-.46	-.32	+1.0

Table 6.82: R-squared from the Analyses of variance for nominal APIs, reported by the class-valued API in ecosection M333d.

M333d: R-squared for Nominal Indices by Class-valued Indices										
Class-Valued Indices	RRSV	WP-BRH	WP-BRP	DMDF	DMW-L	DM-LP	WSB-W	DCY-ET	DCY-LP	DCYO-T
DFBGR	0.002	0.012	0.003	0.191	0.003	0.006	0.089	0.005	0.004	0.078
MPBLP	0.020	0.029	0.008	0.047	0.004	0.638	0.034	0.090	0.292	0.048
MPBPP	0.006	0.035	0.004	0.018	0.018	0.002	0.028	0.019	0.004	0.042
MP-BWP	0.005	0.083	0.089	0.006	0.030	0.036	0.007	0.043	0.027	0.000
SB	0.000	0.013	0.008	0.048	0.010	0.012	0.015	0.035	0.015	0.033
WSBW	0.009	0.211	0.022	0.046	0.051	0.026	0.009	0.026	0.009	0.044

For the pairs of class valued APIs in zone M333d the following table presents the significance level of the Chi-square test for independence. Only APIs for different agents are tested against one another.

Table 6.83: Significance level for Chi-square tests comparing class-valued APIs in ecosection M333d.

M333d: Significance Levels from Chi-square Test for Class-valued APIs								
	DF-BGR	DF-BWD	MP-BLP	LPR-OLE	MP-BPP	PPRO-LE	MP-BWP	SB
MP-BLP	0.005	0.000						
LPRO-LE	0.000	0.000						
MPBPP	0.002	0.000	0.615	0.000				
PPRO-LE	0.000	0.000	0.018	0.000				
MP-BWP	0.000	0.000	0.000	0.000	0.168	0.000		
SB	0.181	0.019	0.127	0.000	0.262	0.079	0.002	
WSBW	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

SIGNIFICANT COMBINATIONS OF AGENTS AND MULTI-AGENT FUNCTIONS

by Susan Hagle

Action Probability Index (API) Patterns

The majority of polygons in our samples had conditions that could support a variety of pathogen and insect activities. The API, or action probability index, is a measure of the relative probability that a particular pathogen or insect will cause significant changes in vegetation. In the 1975-era survey, 87 percent of hectares in M332a and 96 percent of M333d had a moderate to high probability of significant effect from at least one of the pathogens and insects analyzed. Based on the co-occurrence of moderate to high API levels for two or more pathogens and insects, combined effects in the 1975 era were indicated in 60 percent and 62 percent of hectares in M332a and M333d, respectively. Nine pairs of pathogens and/or insect APIs co-occurred in at least 5 percent of hectares of each of the ecosections (Tables 6.89 and 6.90).

Table 6.89: Co-occurrence of moderate to high index values for insects and pathogens in 1975-era survey of sample polygons for ecosection M332a.

First Agent		Second Agent	% ha.
Douglas-fir dwarf mistletoe	and	Severe root disease	21
Severe root disease	and	Stem decay in true firs/hemlocks	13
Douglas-fir dwarf mistletoe	and	Douglas-fir beetle group	13
Douglas-fir beetle group	and	Severe root disease	12
Spruce beetle	and	Severe root disease	11
Stem decay in lodgepole pine	and	Mountain pine beetle in lodgepole pine	7
Spruce beetle	and	Stem decay in true firs/hemlocks	7
Douglas-fir dwarf mistletoe	and	Mountain pine beetle in ponderosa pine	5
Douglas-fir dwarf mistletoe	and	Western spruce budworm	5

Table 6.90: Co-occurrence of moderate to high index values for insects and pathogens in 1975-era survey of sample polygons for ecosection M333d.

First Agent		Second Agent	% ha.
Douglas-fir dwarf mistletoe	and	Root disease severity	16
Root disease severity	and	Mountain pine beetle in western white pine	11
White pine blister rust probability	and	Douglas-fir beetle group	8
White pine blister rust probability	and	Mountain pine beetle in western white pine	7
Stem decay in true firs/hemlocks	and	Mountain pine beetle in western white pine	7
Douglas-fir dwarf mistletoe	and	Western spruce budworm	6
Douglas-fir beetle group	and	Douglas-fir dwarf mistletoe	6
Root disease severity	and	Douglas-fir beetle group	5
Root disease severity	and	Lodgepole pine dwarf mistletoe	5

In most cases, although the agents were predicted to occur in the same polygons, the variance of their indices were not correlated nor dependent. It also was somewhat more common for APIs to be negatively correlated than positively correlated. For example, in M332a, seven out of 90 pairs of APIs tested had positive correlation coefficients of .20 or more while nine had negative coefficients of at least -.20 (Table 6.81). Likewise, in M333d, six of 90 pairs had positive coefficients of .20 or more and eight had negative coefficients of at least -.20 (Table 6.86). In most cases negative correlations are because of requirements for different hosts or different structural stages in stands. For example, APIs in both ecosections for Douglas-fir dwarf mistletoe and lodgepole pine dwarf mistletoe are negatively correlated, as are those of Douglas-fir dwarf mistletoe and stem decay of true firs and hemlocks (Tables 6.81 and 6.86). The twelve pairs of APIs which had the most significant positive correlations or dependence are summarized in Table 6.91.

Table 6.91: Action probability indices that exhibit positive correlations or significant dependence. Results summarized from Tables 6.81 through 6.88.

Ecosection	Variable 1	Variable 2	Test	Value
M332a	Root disease severity	White pine blister rust hazard	ANOVA*; Cor. Coeff.	.49
	Stem decay of lodgepole pine	Lodgepole pine dwarf mistletoe	ANOVA; Cor. Coeff.	.78
	"Other" Stem decay	Douglas-fir dwarf mistletoe	ANOVA; Cor. Coeff.	.55
	Mountain pine beetle in lodgepole pine	Lodgepole pine dwarf mistletoe	ANOVA; R-squared	.49
	Mountain pine beetle in lodgepole pine	Stem decay of lodgepole pine	ANOVA; R-squared	.51
	Western spruce budworm	Douglas-fir beetle group	ANOVA; R-squared	.30
	Douglas-fir beetle group	Western spruce budworm	Chi-squared; Significance	.00
M333d	Western spruce budworm	Douglas-fir dwarf mistletoe	ANOVA; Cor. Coeff.	.40
	Stem decay of lodgepole pine	Lodgepole pine dwarf mistletoe	ANOVA; Cor. Coeff.	.66
	Stem decay "other"	Douglas-fir beetle group	ANOVA; Cor. Coeff.	.66
	Mountain pine beetle in lodgepole pine	Lodgepole pine dwarf mistletoe	ANOVA; R-squared	.64
	Douglas-fir beetle group	Western spruce budworm	Chi-squared; Significance	.00

*ANOVA: Analysis of Variance

Polygons with high Douglas-fir beetle group action probability. In ecosection M332a, 1,614 hectares had API values greater than zero for Douglas-fir beetle group action (DFBGR), root disease (RRSV), and Douglas-fir dwarf mistletoe (DMDF). In those polygons of M332a where DFBGR was high (H), the average RRSV was 4.0 and the average DMDF was 4.2. An average RRSV of 4.0 is slightly higher than the overall average (3.7) for this ecosection, but the 4.7 average for DMDF is much higher than the overall average of 2.4. Analysis of

variance also detected a somewhat stronger relationship between DMDF and DFBGR (R-squared = .211), compared to RRSV and DFBGR (R-squared = .002) (Table 6.83).

A similar pattern is seen in ecosection M333d. Of 2,013 hectares where Douglas-fir beetle group API is moderate to high, Douglas-fir dwarf mistletoe, root diseases, white pine blister rust, larch dwarf mistletoe, stem decay "other," western spruce budworm, mountain pine beetle in western white pine, and stem decay caused by *E. tinctorium* all have significant potential effects as well (Table 6.92).

Table 6.92: Co-occurrence of other pathogen and insect APIs in polygons rated as moderate to high probability of Douglas-fir beetle group action in ecosection M333d.

Pathogen or Insect	% of ha. with API>0	Average API	Range (Max. Possible)	Class Frequency
Douglas-fir dwarf mistletoe	100	4.1	1-6 (6)	
Root disease	90	4.0	0-9 (9)	
Western larch dwarf mistletoe	71	1.0	0-3 (6)	
"Other" stem decay	66	0.9	0-3 (3)	
Western spruce budworm	50	3.0	0-10 (10)	
E. tinctorium decay	23	1.5	0-10 (11)	
Mountain pine beetle in whitebark pine	44			H = 5%, M = 37%, L = 2%, 0 = 56%

In M333d polygons that were rated high for Douglas-fir beetle group action (1,567 hectares in 39 polygon classes), Douglas-fir dwarf mistletoe action probability was also at least 1 on all hectares and root disease severity was at least 1 on 90 percent of hectares. The root disease severity average was 4.0 and the Douglas-fir dwarf mistletoe average was 4.2. The average RRSV in this group was the same as the overall average for the ecosection, but the 4.2 average for Douglas-fir dwarf mistletoe was much higher than the overall average of 1.8. The variance of the dwarf mistletoe API (Table 6.87) was again somewhat better accounted for by the DFBGR (R-squared =.191) than was that of RRSV (R-squared = .002) .

Both Douglas-fir beetle and Douglas-fir dwarf mistletoe require stands with a large component of Douglas-fir, with effects increasing as stands mature. Root pathogens, on the other hand, are very significant in true fir stands as well as Douglas-fir, and they generally reduce the average age and diameter of trees in stands by killing trees of all ages and sizes. Thus the most severe root disease conditions are generally found in stands in which root disease has killed most of the mature trees (if any had reach maturity), leaving more recently regenerated trees as the

primary stand component. This probably also accounts for the lack of correlation between Douglas-fir dwarf mistletoe probability and root disease severity (Tables 6.81 and 6.86).

The group of polygons with Douglas-fir cover type and mature, closed canopy structure class (3) is particularly prone to a variety of insects and pathogens. All of the stands in this class had high probabilities for Douglas-fir beetle; the Douglas-fir dwarf mistletoe APIs averaged 4.7 (range 4-6); the root disease severity averaged 3.8 (range 2-6); nearly all of the polygons rated high for western spruce budworm effect; and the average probability for stem decay was moderate. With so much potential insect and pathogen activity, it is easy to understand why mature, closed canopied stands of Douglas-fir were uncommon in our samples of both 1935 and 1975 eras, although an abundance of Douglas-fir recruitment occurs over a wide range of site types. By the 1975 era, 18 percent of our sample of M332a was Douglas-fir cover type but only 2.5 percent was Douglas-fir cover type in structure class 3.

Polygons with white pine blister rust and root disease. Root disease severity levels and white pine blister rust hazard were fairly well correlated in M333d, with a coefficient of +.39, but the probability of current effect from white pine blister rust (WPBR risk) was not correlated with root disease severity (coefficient = -.02). The rust hazard was based on habitat types that are particularly conducive to rust infection, while the rust risk rating was based on both habitat type and presence of susceptible white pine trees. The positive correlation of root disease severity with rust hazard is expected since both diseases area prone to be most severe on relatively warm and moist sites. Past activity of white pine blister rust, removing much of the white pine component from these productive sites, probably shifted the composition toward more root disease susceptible species in many polygons (Byler et al. 1994). Of course, in stands with large components of root disease-resistant white pine, root disease severity is expected to be less. This is evident in the non-correlation between WPBR risk and root disease severity.

Of 116 polygons, 3,102 hectares of M333d on which the probable effect from white pine blister rust was moderate to high (WPBRP greater than 4), only five polygons (159 hectares) had no apparent root disease. A little more than half (56 percent) of the polygons with moderate to high blister rust probabilities also had high to moderate root disease severity. The indices for blister rust and root disease were not, however, correlated with coefficients for blister rust hazard, and blister rust probability both very small (Table 6.86). In fact, the average root disease severity for hectares with moderate to high blister rust probability (3.5) was lower than the average for the ecosection (4.0). The presence of root disease on most polygons with blister rust is expected because white pine is most prevalent in habitat type groups 4 through 7, which are also the groups most affected by root disease. These sites provide optimum conditions for both pathogens. The probability index for blister rust is highest for young stands with a large component of white pine. Western white pine is relatively resistant to root disease, and it's presence generally will reduce the severity of root disease proportionately on a site. Also, young stands, even of fairly susceptible species, generally rate fairly low for root disease unless they are clearly the result of regeneration within a root disease patch. So the blister rust probability index would not be expected to correlate with root disease severity.

Mountain pine beetle, dwarf mistletoe and stem decay in lodgepole pine. Lodgepole pine cover type in structure classes 2, 3, and 4 (986 hectares) all had at least a low level of mountain pine beetle probability (MPBLP greater than zero) and lodgepole pine dwarf mistletoe (DMLP >0). Fifty-five percent of hectares in this group had moderate to high probabilities of

mountain pine beetle actions, and the lodgepole pine dwarf mistletoe APIs averaged 4, compared to the overall average for M332a of 1. Analysis of variance demonstrated that 50 percent of the variation in lodgepole pine dwarf mistletoe was accounted for in the API classes for mountain pine beetle (Table 6.83). Similar hosts and stands conditions for maximum effect account for this close correspondence in mountain pine beetle and lodgepole pine dwarf mistletoe.

Polygons in M332a that had a high level of probability for stem decay in lodgepole pine (DCYLP = 3) also had a very high average probability for lodgepole pine dwarf mistletoe (5.8). In fact, the correlation coefficient for DCYLP and DMLP was .78 (Table 6.81). The coefficient for these APIs in M333d was also quite high, .66, but there were few hectares with high probability of stem decay in lodgepole pine. Again, these agents effect the same host and increase in intensity with stand age, so their correlation is expected.

Succession Function Patterns

Succession function patterns were somewhat related to the API patterns, but not reliably so. Herein lies the distinction between the action probability index and succession function index. The action probability index identifies polygons with conditions conducive for potentially significant actions by pathogens and insects. The function index identifies the relative probability that the pathogen or insect significantly influences succession in a class of polygons. This is based on analyses which compare the successional outcomes for a class of polygons with their APIs. Pathogens and insects with moderate to high APIs in a given polygon class are considered potentially active. The proportion of polygons with successional outcomes which are logically a result of the insect or pathogen (or combination) are assigned a relative probability of successional effect. The index ranges from 0 to 3, with 0 indicating that the insect or pathogen had very little likelihood of causing the observed outcome and 3 indicating a high probability that most of the observed outcome was a direct result of the insect or pathogen. Function index values of 2 or 3 are considered to indicate a moderate to high probable successional effect.

Based on proportions within polygons classes, combined effects of two or more types of pathogens or insects were calculated to have been likely on roughly 65 percent of hectares in M332a and 50 percent in M333d from 1935 to 1975 eras. Such combined effects probably account for much of the observed variability in succession patterns.

Where more than one pathogen or insect species is active in a stand, their immediate effects may be similar, thereby additive, or they may have opposing effects, with outcomes which may differ from that which results from either agent acting alone. Many examples of both types of combined functions were observed in ecosection M332a and M333d.

Additive functions

Root diseases and Douglas-fir beetle. Root diseases and Douglas-fir beetle produced the most significant combined function with complementary effects on succession detected in our analysis of M332a. This combined function was seen on 16 percent of hectares. The outcomes were about evenly divided among preventing crown closure, pushing the species composition toward climax, maintain early seral species, and stalling the structure in an immature stage (Figure 6.73). The combination of Douglas-fir beetle and root disease accounted for over half of the hectares on which the early seral species were maintained while canopy closure was prevented. Similarly, over a third of hectares on which early seral species were maintained while the structure reverted to an immature stage were primarily influenced by the combination of Douglas-fir beetle and root disease (Figure 6.74).

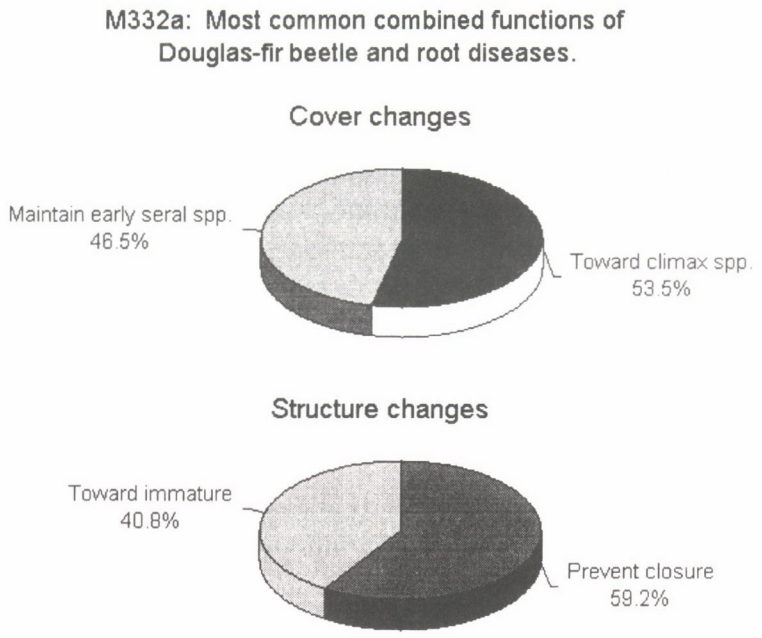

Figure 6.73: Most common combined functions of Douglas-fir beetle and root diseases, M332a.

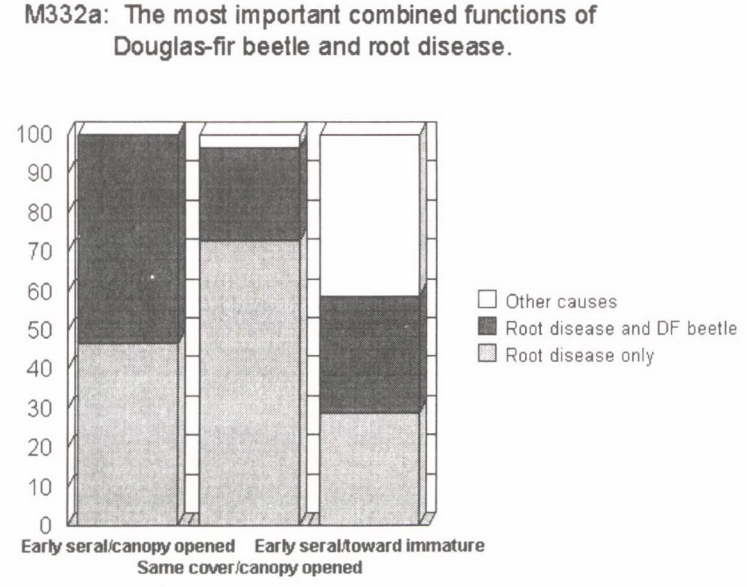

Figure 6.74: Most important combined functions of Douglas-fir beetle and root disease.

It was fairly rare for Douglas-fir beetle to have significant function in the absence of root diseases, but it did occur on 3 percent of hectares in M332a, (and less than 1 percent of M333d)

during the 40-year study interval. Douglas-fir beetle acting alone also distributed outcomes about equally among pushing to climax, preventing canopy closure, and stalling in immature structure classes. Root pathogens acting without strong Douglas-fir beetle influences had a relatively greater tendency to push toward climax or stall structure in the immature stages than did the combination of root pathogens and Douglas-fir beetle (Table 6.93). The relatively slow action of root disease in creating canopy openings may account for the greater tendency to push toward shade-tolerant species, compared to the more abrupt group-killing action of Douglas-fir beetle. Root pathogens kill trees of all ages and sizes, whereas Douglas-fir beetles require much larger diameters to support brood production; therefore, it is not surprising that root pathogens are more commonly seen acting alone in stands that are stalled in immature structure classes.

Table 6.93: Combined successional outcomes with and without moderate to high Douglas-fir beetle probability in polygons with moderate to high root disease severity.

	Primary Cover Effects (proportion)	Primary Structure Effects (proportion)
M332a: Structure Classes 2, 3, and 4		
Root disease with Douglas-fir beetle	Increase or maintain early seral (.39) Increase climax (.38) No change in cover (.24)	Prevent closure (.42) Toward immature (.29) No effect on structure (.29)
Root disease without Douglas-fir beetle	Increase climax (.54) Increase or maintain early seral (.27) No change in cover (.21)	No effect on structure (.53) Toward immature (.17) Prevent closure (.17) Stall in young/small (.11)
M333d: Structure Classes 2, 3, and 4		
Root disease with Douglas-fir beetle	Increase climax (.63) Increase or maintain early seral (.21) No change in cover (.16)	Prevent closure (.59) Toward immature (.29) No effect on structure (.12)
Root disease without Douglas-fir beetle	Increase climax (.75) Increase or maintain early seral (.23)	Toward immature (.39) Stall in young/small (.29) No effect on structure (.17) Prevent closure (.15)

Mountain pine beetle and lodgepole pine dwarf mistletoe. Mountain pine beetle and lodgepole pine dwarf mistletoe are probably competitors under conditions of high population levels of either species. Dwarf mistletoe reduces the growth and vigor of heavily infected trees. This, generally results in thinner phloem which is less conducive to healthy brood production for mountain pine beetles. Stands that are heavily infested with lodgepole pine dwarf mistletoe tend to be marginal habitat for mountain pine beetle. This probably explains the greater survival of lodgepole pine where both had moderate to high probabilities, compared to stands where

mountain pine beetles were expected to be acting alone (Table 6.94). With mountain pine beetles alone, most stands changed substantially to subalpine fir with half becoming low-density or small tree stands. That is, as much of the mature lodgepole pine component was killed, the live stand composition shifted toward the understory of subalpine fir or other late seral species. Among the stands that were rated moderate to high for lodgepole pine dwarf mistletoe, those which were not rated moderate to high for mountain pine beetle as well generally did not meet the minimum average DBH for the lodgepole pine component. In the face of dwarf mistletoe alone, these stands tended to remain small diameter or lose the larger trees, moving to toward small average tree sizes. Although there was also a tendency for these stands to increase in later seral components, the survival of the lodgepole pine component appears to be much higher than in those stands that had high mountain pine beetle probabilities but no dwarf mistletoe.

Table 6.94: Combined successional outcomes of lodgepole pine dwarf mistletoe and mountain pine beetle. Polygons with moderate to high probabilities of either or both APIs.

M332a: Structure Classes 2, 3, and 4	Primary Cover Effects (proportion)	Primary Structure Effects (proportion)
Mountain pine beetle with lodgepole pine dwarf mistletoe	Increase climax (.47) Maintain early seral (.48)	No effect on structure (.86)
Mountain pine beetle without lodgepole pine dwarf mistletoe	Increase climax (.80) Increase or maintain early seral (.10) No change in cover (.09)	No effect on structure (.50) Toward immature (.25) Prevent closure (.20)
Lodgepole pine dwarf mistletoe without mountain pine beetle	Increase climax (.62) Maintain early seral (.38)	Toward immature (.50) No effect on structure (.40) Stall in young/small (.11)

Root disease and Douglas-fir dwarf mistletoe. Moderate to high APIs for Douglas-fir dwarf mistletoe were most common in structure classes 2, 3, and 4 and habitat type groups 2, 3, 4, and 5 in M332a; similarly they were most common in structure classes 2 and 4 and habitat type groups 2, 4, and 5 in M333d. The average root disease severity in polygons rated moderate to high for Douglas-fir dwarf mistletoe probability was nearly the same as those rated lower for mistletoe probability (3.8 and 3.6, respectively). Likewise, the average Douglas-fir dwarf mistletoe probability was nearly the same whether the root disease severity was high or low (DMDF = 2.4 and 2.3, respectively).

Both root pathogens and dwarf mistletoes have very strong tendencies to cause long-term, chronic diseases in stands, so that any stand that is significantly influenced by either of these pathogens is likely to have developed on previously-infested sites. Also, both pathogens reduce growth and increase mortality rates of Douglas-fir. There were some differences in outcome in stands that had moderate to high probabilities of both root disease and Douglas-fir dwarf mistletoe, compared to those thought to have been effected by root disease without dwarf mistletoe (Table 6.95). For the most part, these differences could be explained on the basis of lower reproduction rates of Douglas-fir that have heavy dwarf mistletoe infections. This is seen as an additive effect in increasing or maintaining pines or larch in the stands. This effect was

confounded in M333d by a fairly large proportion of the seral component being western white pine, which was killed at a high rate by blister rust. Most of the early seral components that survived in polygons with all three pathogens were western larch or lodgepole pine.

The combined effects of dwarf mistletoe and root disease was very likely to have prevented canopy closure from occurring, as seen on 78 percent of affected hectares in M332a and 98 percent of those in M333d.

Table 6.95: Combined successional outcomes with and without moderate to high Douglas-fir dwarf mistletoe probability in polygons with moderate to high root disease severity.

	Primary Cover Effects (proportion)	Primary Structure Effects (proportion)
M332a: Structure Classes 2, 3, and 4		
Root disease with Douglas-fir dwarf mistletoe	Increase climax (.49) No change in cover (.26) Increase or maintain early seral (.25)	Prevent closure (.78) No effect on structure (.21)
Root disease without Douglas-fir dwarf mistletoe	Increase climax (.71) Increase or maintain early seral (.20) No change in cover (.09)	Toward immature (.33) No effect on structure (.31) Stall in young/small (.22) Prevent closure (.14)
M333d: Structure Classes 2 and 4		
Root disease with Douglas-fir dwarf mistletoe	Increase climax (.69) No change in cover (.20) Increase or maintain early seral (.11)	Prevent closure (.98)
Root disease without Douglas-fir dwarf mistletoe	Increase climax (.75) Increase or maintain early seral (.23)	Stall in young/small (.34) No effect on structure (.32) Prevent closure (.20) Toward immature (.14)

White pine blister rust and mountain pine beetle in western white pine. The effects of white pine blister rust, with and without mountain pine beetle indicated, are very similar (Table 6.96). The effects of these two species is likely additive with both being highly prevalent during the 40-year study period.

Table 6.96: Combined successional outcomes with and without moderate to high Mountain pine beetle probability in polygons with moderate to high white pine blister rust.

M333d: Structure Classes 3 and 4	Primary Cover Effects (proportion)	Primary Structure Effects (proportion)
White pine blister rust with mountain pine beetle	Increase climax (.86) Increase or maintain early seral (.14)	No effect on structure (.55) Decrease density (.27) Prevent closure (.98) Toward immature (.17)
White pine blister rust without mountain pine beetle	Increase climax (.82) Increase or maintain early seral (.19)	No effect on structure (.65) Toward immature (.25) Prevent closure (.10)

Opposing actions

We found numerous examples of insects and pathogens with correlated indices that had opposing succession functions: for example, stands with high probabilities for bark beetles removing mature ponderosa pine as well as high probabilities for root disease reducing the Douglas-fir component. Within the group of polygons that had as least a low probability for bark beetle effect on ponderosa pine, only 2 percent of M332a and 15 percent of M333d had no evidence of root disease. What's more, the root disease severity increased with increasing probability of bark beetle activity in ponderosa pine (Table 6.97). Among the criteria for the API for bark beetles in ponderosa pine, the proportion of the basal area which is ponderosa pine and the average diameter of ponderosa pine are important attributes.

Bark beetles of ponderosa pine and root disease of Douglas-fir. Root disease severity is a measure of the past activity of root pathogens in the stand, the cumulative effect of root disease. Because of this, the higher the root disease severity, the more the species composition may have been shifted to root disease-resistant species, such as ponderosa pine. It is likely that long-term effects from root disease will also include improved growth in resistant species because of the reduction in competition, resulting in increased average tree diameters. So, it is not surprising that as root disease severity increases, the probability of bark beetle effects in ponderosa pine may also increase. While both root disease and ponderosa pine bark beetles tend to push the structure class toward smaller trees and open canopy conditions (structure class 2 or 4), root disease will favor ponderosa pine while pine beetles will favor Douglas-fir. Patterns of regeneration in the absence of fire also favors Douglas-fir.

Table 6.97: Average root disease severity by ponderosa pine bark beetle API.

PP Bark Beetle API	M332a Avg. RRSV	M333d Avg. RRSV
H	5.0	4.5
M	3.7	4.0
L	2.7	3.1

The changes that occurred in polygons classified as mixed ponderosa pine and Douglas-fir in the 1935 era (cover type 2) were indicative of the range of effects from the combination of root disease and ponderosa pine bark beetles. In M332a, 60 percent of hectares that began in cover type 2 with structure class 2 in the 1935 era, were still in this class in the 1975 era (Table 6.98). Forty-four percent of hectares in M333d followed this path. This outcome is consistent with enough root disease effect to favor retention of ponderosa pine while preventing the average diameter of Douglas-fir from increasing substantially, in combination with bark beetles preventing substantial increases in the average diameter of ponderosa pine without killing enough pine to reduce them to less than 25 percent of the stand cubic volume. In both ecosections, most of the remaining hectares in CT2/SC 2 in the 1935 era were either Douglas-fir or true fir cover types in the 1975 era. The patterns are similar in structure class 4 of this cover type (Table 6.98).

Table 6.98: Cover type changes in polygons which were ponderosa pine/Douglas-fir mixed cover type (code CT 2) in the 1935 era.

1935-era Cover Type	1935-era Structure Class	1975-era Cover Type	M332a (%)*	M333d (%)
2	2	2	60	44
		5 (minor amount in 9)	40	48
	4	2	29	29
		2.8	3	7
		3	0	9
		5	48	15
		9 or 11	20	20
		Others (all <10%)	0	20

* Percent of total hectares in the 1935-era cover type/structure class

Structure class changes were also consistent with activity from both pine bark beetles and root disease. Although a few hectares increased in stocking or size to become structure class 3, most either remained low stocking (less than 13,000 board feet/acre, relegating polygons to structure class 4) or dropped below the threshold for sawlog-size stands (at least 50 percent of the cubic foot volume in trees at least 12 inches DBH), becoming or remaining structure class 2 (Table 6.99). With the requirements for structure class 3 fairly low (at least 13,000 board feet/acre and at least 50 percent of the cubic foot volume in trees at least 12 inches DBH), most of the stands in our sample would likely have reach structure class 3 over a 40-year period in the absence of significant perturbations. This is particularly true of those which were in structure class 4 in the 1935 era, having already met the size requirement and starting with a minimum of 3000 bdft/acre (Tables 2.6 and 2.7).

Table 6.99: Structure class changes in polygons which were ponderosa pine/Douglas-fir mixed cover type (code CT 2) in the 1935 era.

1935-era Cover Type	1935-era Structure class	1975-era Structure class	M332a (%)*	M333d (%)
2	2	2	0	49
		3	10	0
		4	90	51
	4	2	37	38
		3	14	25
		4	49	37

* Percent of total hectares in the 1935-era cover type/structure class

White pine blister rust and root disease. The highest levels of blister rust activity probably largely predated the higher levels of root disease activity in individual stands. As the white pine component was killed and the Douglas-fir and grand fir components increased in importance, the root disease activity increased. The net result over the 40-year interval indicated very significant combined functions for the pathogens. White pine blister rust and root pathogens were a particularly common combination in M333d. One of the most dramatic functions observed accounted for a large proportion of the sample hectares which were stalled in immature structures for 40 years (Figure 6.84). This stalling of structure is likely the result of nearly complete removal the young western white pine in these stands by blister rust while root pathogens killed Douglas-fir and grand fir on an ongoing basis. The result is a perpetually young, perpetually well-stocked stand composed mostly of Douglas-fir and grand fir. This is reflected in most of the polygons (76 percent) in which this combined function occurred having a major component of Douglas-fir and/or grand fir at the time of the 1975-era survey. It is likely that this combined function will continue to occur in these polygons for several decades beyond the 1975 era.

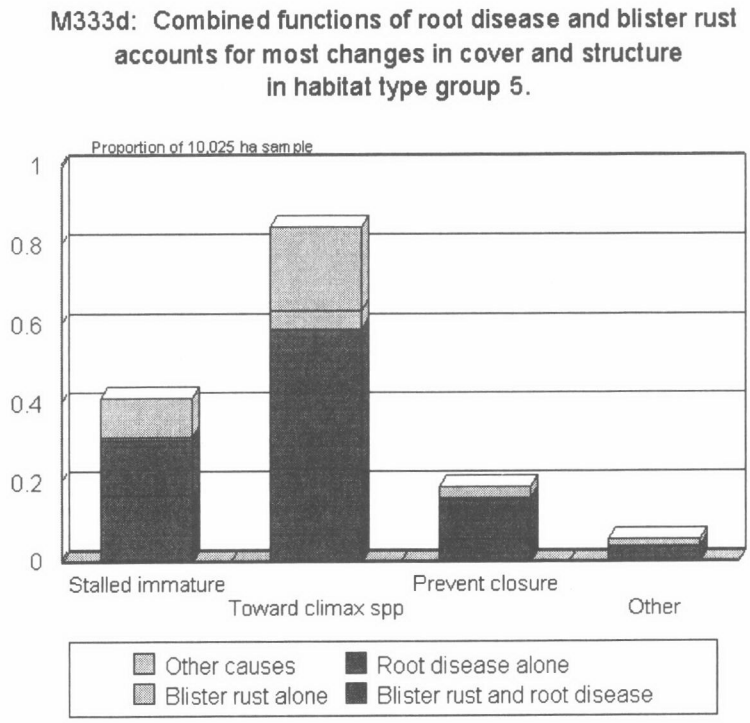

Figure 6.75: Combined functions of root disease and blister rust in changes in cover and structure in habitat type group 5, M333d.

Root pathogens acting without significant white pine blister rust and blister rust without significant root pathogen influence, both had more of a tendency to push toward climax (Table 6.100). The combination of these agents was more likely to stall structures in the immature than either of the agents independently. It appears likely that the introduction of white pine blister rust has significantly altered the balance of these major classes of succession functions, shifting the balance toward structure classes indicative of both low timber volume productivity and low density of mature canopy.

Table 6.100: Combined successional outcomes with and without moderate to high root disease severity in polygons with white pine cover type and moderate to high white pine blister rust.

M333d: White Pine Cover Types	Primary Cover Effects (proportion)	Primary Structure Effects (proportion)
White pine blister rust with root disease	Increase climax (.61) Increase or maintain early seral (.33)	No effect on structure (.49) Toward immature (.19) Prevent closure (.12) Stall in young/small (.11) Decrease density (.10)
White pine blister rust without root disease	Increase climax (.58) Maintain early seral (.42)	No effect on structure (.60) Toward immature (.23) Prevent closure (.15)

SECTION 7: SUMMARY AND CONCLUSIONS
Overall Trends in Ecosections M332a and M333d

By Susan Hagle

Most our sample of ecosections M332a and M333d underwent changes in cover, structure, or both between 1935 and 1975 eras. In most cases, pathogens and insects were indicated as having altered the course or timing of succession. Over 90 percent of hectares in M332a underwent such successional stage changes, with 80 percent of these changes attributable to pathogens and insects. In the sample of M333d, 95 percent changed successional stage, with 75 percent of the changes attributable to pathogens and insects. From 98 1935-era polygon classes (based on habitat type group, cover type, and structure class) in M332a, we observed 266 unique successional pathways, an average of 2.7 types of transitions per polygon class. There were from one to eight distinct transitions for each polygon class. Of 148 1935-era polygon classes in M333d, 743 pathways occurred in our sample, averaging 5 types of transitions per polygon class, with a range of 1 to 27 distinct transitions for each class.

In both ecosections, a change toward later seral cover types, larger-tree structure classes and greater stand density was most prevalent. The most common function of pathogens and insects was to accelerate the change to later seral species compositions. An ecologically important function of many insects and pathogens was to cause prolonged retention of early seral species. This function occurred on 25 percent and 23 percent of hectares, respectively, in M332a and M333d.

Several unique successional pathways were identified that, without human intervention, probably require the actions of a particular pathogen or insect. One such pathway is seen in mature late-seral or climax species cover types with low basal area (structure class 4) on warm, moderate, or moist habitat types (groups 3, 4, and 5). When these polygon classes retained the same cover type while remaining in an open or broken canopy condition (also low basal area) for the 40-year interval, stem decay was found to be the only significant agent indicated in maintaining this condition. Similarly, when Douglas-fir or grand fir cover types in seedling/sapling structure remained so for the 40-year sample period, root disease was the only mechanism indicated: root disease severity was generally very high under these conditions.

In several types of transitions, combinations of pathogens and insects were seen to have opposing effects on forest succession. For example, the combination of root pathogens and mountain pine beetle in mixed ponderosa pine/Douglas-fir stands in habitat type group 2 resulted in low-density stands with Douglas-fir cover type (structure class 4) or small-diameter stands (structure classes 1 or 2) of ponderosa pine/Douglas-fir cover type. Both transitions are likely due to reduction of the large-tree components of Douglas-fir (by root pathogens) and ponderosa pine (by bark beetles) followed by regeneration of Douglas-fir, in particular.

Another interesting example was seen in cover or forest types with a significant western larch component in M333d. In habitat type groups 3, 4, and 5, the moderate to moist and warm habitats, the outcome after 40 years was nearly always a loss of most of the larch component and resulting low canopy density. In this case, the combined effects of blister rust, root disease, and bark beetles reduced the usually important western white pine, Douglas-fir and grand fir components which should have increased the relative importance of western larch. Instead, the polygons lost most of the larch component, changing to late-seral or near-climax species cover types while remaining in low density conditions. Western larch dwarf mistletoe was indicated as highly involved in the decline of larch.

TRENDS IN COVER AND STRUCTURE

In the sample of ecosection M332a, moderately warm and dry to cool and moist habitat types (groups 2, 4, 5, and 7) were best represented. Douglas-fir was the most common single forest type in the 1975-era survey, as well as the most common component in combination forest types, followed by subalpine fir, lodgepole pine, and grand fir. "Alpine," Douglas-fir, western redcedar/grand fir, ponderosa pine-mixture, and lodgepole pine cover types were most commonly assigned to these 1975-era polygons (ranging from 27 percent to 13 percent). The 1935-era cover types on these same hectares were mostly lodgepole pine, Douglas-fir, or ponderosa pine (ranging from 21 percent to 14 percent) (Table 5.17). Structure class distribution remained fairly consistent between 1935 and 1975 eras. The only notable changes were a drop from 8 percent to 2 percent in nonforested hectares, and a doubling (from 10 percent to 20 percent) of the large-tree, well-stocked structure class (SC 3). Pole-size, moderately to well-stocked stands were most common, making up 41 percent of the sample in the 1935 era and 40 percent in the 1975 era (Table 5.14).

Habitat types in the M333d sample tended to be cooler types. Most common were habitat type groups 5, 7, and 9. Forest types were diverse in the 1975 era, with Douglas-fir slightly more common than others–occurring on 10 percent of hectares as a single-species forest type. Pole-size to large-tree structure classes were most common in the 1975 era. In the 1935 era, this sample was mostly large trees with low stocking (SC 4), seedling or sapling size stands, or nonforested because of fire. Cover type shifted from mostly white pine, larch mixtures, or nonforested land in the 1935 era (ranging from 35 percent to 16 percent) to "alpine," white pine, lodgepole pine, western hemlock/grand fir, or Douglas-fir (ranging from 25 percent to 11 percent).

OVERALL TRENDS IN PATHOGEN AND INSECT FUNCTIONS

Prevalent Functions in M332a

In M332a, the most significant influences from 1935 to 1975 eras were from root diseases, mountain pine beetle in lodgepole pine, and Douglas-fir beetle (Table 7.1). Unlike M333d, there was little indication of significant changes in the way pathogens and insects have functioned between 1935 and 1975 eras. This is not to say that their functions are not important; they were considered to be the driving force in over 80 percent of transitions in our sample.

Root diseases were the most widespread and influential of the insects and pathogens included in this analysis. All but 2 percent of polygons were to seen to have some level of root disease effect in the 1975 era. The average severity was 3.2, within the range of 0 to 8. Root disease severities were highest in habitat groups 3, 4, 5, and 7, and the cover types with the highest average severity were western redcedar/grand fir, western redcedar, western larch mixtures, and ponderosa pine mixtures. These were cover types that were often produced when severe root disease disproportionately killed Douglas-fir and grand fir components, thereby shifting composition toward the later-seral or climax species or increasing the retention of other earlier seral species. The overall average root disease severity probably increased from a little less than 3 in the 1935 era to the 3.2 measured in the 1975 era. This trend appears likely to continue through 2015, when the average may be close to 4 (Table 6.40).

Both weeding and group-killing types of Douglas-fir beetle actions were fairly common in M332a, with 14 percent of hectares rated as having moderate to high probability of significant influence from Douglas-fir beetle. On habitat types where Douglas-fir is climax, Douglas-fir beetle generally either reduced the density of large-diameter stands or removed enough of the large-diameter trees to cause regression to small-tree structure classes. The cover type generally remained Douglas-fir. On the wetter habitat types, the cover type generally moved toward more grand fir, western redcedar, or western hemlock, while the large-tree structure was retained, often increasing in density.

Douglas-fir beetle and root disease were often active in the same polygons and are known to occur in the same individual trees in many situations (Goheen and Hansen 1993). The most prevalent function of this combination was to retain relatively more ponderosa pine in affected stands thereby prolonging the early seral stages of succession. Where root diseases acted with little influence from Douglas-fir beetle, they were more likely to cause the structure to regress from large-tree to small-tree structures without changing the cover type.

In habitat type groups 1 and 2, mountain pine beetle in ponderosa pine played a important role in counteracting the advantage root disease would have provided the ponderosa pine component. Root disease alone had a modest tendency to maintain or increase the relative importance of ponderosa pine, but where probabilities of mountain pine beetle activity were moderate to high, polygons were more likely to move toward the late-seral and climax Douglas-fir cover type while regressing to smaller-tree structures or decreasing in stand density.

Dynamics in lodgepole pine cover types were largely driven by mountain pine beetle. All but about 20 percent of hectares in this type underwent transitions in cover or structure that were consistent with outcomes expected from mountain pine beetle activity. Half of the area in our sample that had been identified as lodgepole pine cover type in the 1935 era remained lodgepole pine, however, the stands which were pole-size or larger generally converted to another cover type or lost much of the larger-tree component, changing to small-tree structures or low density, large-tree structures. Those that converted were identified as mostly "alpine" (subalpine fir or mountain hemlock) or Douglas-fir cover types in 1975.

In the 1935 era, about 10 percent of our sample of M332a had a significant component of western white pine or whitebark pine. Less than 1 percent of hectares in this sample now contains a significant component of either of these species. White pine blister rust and mountain pine beetle were implicated in nearly all of these changes in cover type. Most of the polygons that contained white pine or whitebark pine in the 1935 era were in structure classes 1, 2, or 4. Most of these polygons had progressed to late seral or climax species composition by the 1975 era. Cedar or cedar/Douglas-fir mixtures were most common on lower elevation sites, while subalpine fir and mountain hemlock were more likely replacements for white pine and whitebark pine on higher elevation sites. Mountain pine beetle was particularly implicated in the structure class 4 stands, half of which retained a component of whitebark pine in 1975, but none had significant remaining western white pine.

Dwarf mistletoes affecting lodgepole pine, Douglas-fir, and western larch were important influences in a few situations. The stands most affected were those with a large component of host species and were in early to mid-seral stages. Growth suppression and mortality caused by dwarf mistletoes limited stocking density of mature stands while accelerating changes in species composition toward late-seral or climax species. Structure classes 2, 3, and 4 had the highest probability of effect by dwarf mistletoes. In these structure classes, lodgepole pine dwarf mistletoe was indicated as a significant influence on succession in 18 percent of hectares, Douglas-fir

dwarf mistletoe was indicated as significant on 16.5 percent, and larch dwarf mistletoe was significant on 10 percent of hectares in these structure classes. Douglas-fir dwarf mistletoe was implicated in helping retain the early-seral, non-host species in stands, such as ponderosa pine and lodgepole pine. Habitat type groups 2 and 5 were most affected by Douglas-fir dwarf mistletoe. Although larch dwarf mistletoe was implicated in relatively few hectares, the role it played in the decline of mature western larch may have serious long-term ecological impacts through the loss of seed sources and replacement snags for wildlife habitat.

Stem decay effects also appeared to be concentrated in particular polygon classes, affecting a total of 1.7 percent of sample hectares. Stem decay generally develops as stands reach maturity, becoming more advanced as trees age. Breakage of decay-weakened stems results in loss of individual or small clusters of trees. As expected, although they are fairly host-specific, stem decays had little effect on species composition in stands. They functioned to prevent canopy closure in maturing stands or perpetuate broken canopy conditions (structure class 4) in mature stands.

Spruce beetle was also concentrated on certain polygon classes: those with a significant spruce component and structure classes 2, 3, or 4 (mostly SC 3). Overall, about 6 percent of the sample was likely to have been highly influenced by spruce beetle between 1935 and 1975 eras. Spruce beetle outbreaks are usually triggered by windthrow events; without large expanses of spruce blowdown, the outbreaks are generally limited in both time and space. In our sample of M332a, species composition was shifted by spruce beetle outbreaks, resulting in later-seral or climax species, while the structure classes regressed toward younger, smaller trees or lost canopy density, becoming low-density, mature stands (SC 4). These functions were projected to increased to about 15 percent from 1975 to 2015.

Western spruce budworm Action Probability Index (API) was high on 22 percent of hectares in the 1975-era sample. According to polygon classes existing in 1935, approximately 30 percent of hectares probably had high hazard for western spruce budworm defoliation. However, successional pathways were probably affected by budworm on only about 4 percent of hectares. The primary impact of budworm defoliation in M332a is growth loss with limited mortality of small trees. Although these affects are likely to have occurred in the study interval, changes in succession due to budworm occurred in relatively few of the defoliated polygons: primarily those with Douglas-fir forest types. The most common type of successional function was to maintain mature stands in low canopy density conditions without altering the species composition.

Table 7.1: Ecosection M332a; Influences of pathogens and insects from 1935 to 1975 eras.

Pathogen/Insect	Proportion of ha*	Primary Cover Effects (proportion)**	Primary Structure Effects (proportion)
Root pathogens	.47	Increase climax (.70) Maintain early seral (.23)	Toward immature (.38) Prevent closure (.35) No effect (.24)
Mountain pine beetle, lodgepole	.19	Increase climax (.97)	Toward immature (.35) No effect (.29) Prevent closure (.29)

Douglas-fir Beetle	.14	Increase climax (.54) Maintain early seral (.27)	Prevent closure (.46) Toward immature (.23) No effect (.22)
Douglas-fir beetle and root diseases combined	.12	Increase climax (.54) Maintain early seral (.25) No effect (.22)	Prevent closure (.52) No effect (.23) Toward immature (.21)
White pine blister rust	.10	Increase climax (.94)	No effect (.53) Prevent closure (.33)
Bark beetles, ponderosa pine	.06	Increase climax (.78)	Toward immature (.46) Prevent closure (.27)
Mountain pine beetle, white pine	.02	Increase climax (1.0)	Prevent closure (.58) Toward immature (.42)
Douglas-fir dwarf mistletoe	.04	No effect (.50) Maintain early seral (.44)	Prevent closure (1.0)
Lodgepole pine dwarf mistletoe	.01	Increase climax (.98)	Prevent closure (.98)
Western larch dwarf mistletoe	.01	Increase climax (1.0)	Prevent closure (1.0)
Stem decays	.03	Maintain early seral (.52) No effect (.39)	Prevent closure (.64) Decrease density (.30)
Spruce beetle	.01	Maintain early seral (.54) Increase climax (.46)	No effect (.51) Toward immature (.39)
Spruce budworm	.03	Maintain early seral (.46) No effect (.45)	Prevent closure (.84)

*Proportion of hectares in M332a which are expected to be strongly influenced by the pathogen or insect.
**Of the hectares expected to be most affected by the pathogen or insect, the proportion likely to show each successional effect.

Prevalent Functions in M333d

White pine blister rust

The most striking influence in M333d was, not surprisingly, the result of white pine blister rust. The nearly complete conversion of white pine forest types to non-white pine types has been well-documented (Monnig and Byler 1992, Brown and Chojnacky1996). We saw an 88 percent decline in forest types containing a significant component of western white pine in our sample of M333d. Perhaps for the first time, we have been able to document in some detail the forest types and structures to which these white pine forests have changed and the resulting influence these changes have exerted on native pathogens and insects. White pine blister rust was distributed throughout most of the white pine forests of ecosections M332a and M333d by the time of the 1935-era forest survey, so our beginning point data reflect conditions of a forest already afflicted to some extent by the disease. In some locations, the effects may have been significant, while in most they were probably just beginning to alter forest conditions. Large areas of M333d and the northern portion of M332a (where most of the western white pine is found) had burned in the late 1800s and again in 1910. The young white pines growing in these recently burned areas were highly susceptible to white pine blister rust and most probably died quickly

after the rust arrived. By the 1975 era, most of what had been white pine cover type in 1935 had become subalpine fir, western hemlock/grand fir, or western redcedar/grand fir cover types. Douglas-fir was also a highly consistent component of the forest types in these polygons (Table 6.10).

The most common function of white pine blister rust in either western white pine or whitebark pine was to increase the progress toward late-seral or climax species compositions (Table 7.2). Where this took place, the structure of the stands generally remained stalled in seedling or sapling stages or even move backward from large-tree classes to these small-tree structures. Also an important function of blister rust, occurring on about a third of hectares in M333d, was maintaining other seral components of the stands, especially lodgepole pine and western larch. These species apparently took advantage of the resources made available by the death of white pines and increased their relative importance in the species composition. Where this occurred it was usually accompanied by structure class changes to large-diameter tree class with relatively low stocking density or volume production.

With the decline in large-diameter western white pine has come a decline in mountain pine beetle functions in large western white pines. Although there is some activity in younger, smaller white pines in current forests, this is probably quite different from the role mountain pine beetle once played. The abundant large white pine snags created by mountain pine beetle are now a rare occurrence, a loss that may have significant impacts on wildlife species that once utilized the large snags for decades following tree death.

Blister rust and root disease

We have speculated that the loss of white pine to blister rust has been a precursor to severe levels of root disease on much of the productive "white pine type" (Monnig and Byler 1992, Byler et al. 1994, Hagle et al. 1994). Evidence from ecosection M333d supports this view. Sites on which white pine blister rust had been a strong influence between 1935 and 1975 eras were seen to have root disease severities in the 1975 era roughly equal to the overall average of 4, whereas those that had lodgepole pine cover type in the 1935 era average closer to 3 in the 1975 era. When sites with blister rust influence are projected forward to 2015, the root disease severity is expected to decline somewhat to an average of around 3.7, with 40 percent of conversions to western redcedar/grand fir or, western hemlock/grand fir. This future composition is vastly different from the white pine forests of the past, and increasingly different from the Douglas-fir and grand fir mixtures with severe root disease found in our 1975-era sample. Our sample for M333d in the 1935 era included only 2.7 percent of hectares with western redcedar/grand fir (code 8 or 9) or western hemlock/grand fir (code 4); in the 1975 era, these types covered 15.7 percent. The predicted coverage by these types for our sample area in 2015 is 30 percent.

Effects of prevalent functions

The white pine forest "type" may have crossed it's ecological threshold for recovery. With the increase in cedar and hemlock associated with the decrease in white pine, we expect to see future increases in importance of previously unimportant pathogens and insects of cedar and hemlock. These vast changes suggest the possibility that blister rust has caused the forests of the "white pine type" to be deflected toward previously unknown conditions. The long-term development of forests on these sites may lead to unprecedented forest conditions and communities. Friedel (1991) described range conditions on severely degraded sites as having crossed

ecological thresholds, recovery from which would require significant management effort. It is likely that blister rust has created such a situation in which the natural functions of fire and native pathogens and insects will not result in a return to successional pathways which typified these forests at the turn of the century. The longer the delay, the more likely a new trajectory will become, as the genetic makeup of forest communities adapts to the new conditions. Punctuated equilibrium, marked by periods of relatively rapid genetic change, has been associated with changes in ecological conditions (Eldredge and Gould 1972). With the decline of white pine resulting in significant changes in available resources for some of the forest species, the conditions may have been met for Milligan's model for punctuated evolution mediated by "slight changes in the complex distribution of resources" (Milligan 1986). The future on these sites may be very different from the "natural range of variability" model we often cite for acceptable forest conditions.

Impending bark beetle outbreaks in Douglas-fir and grand fir forests. A smaller proportion of 1935-era hectares with white pine cover types converted to mixed stands containing large proportions of grand fir and Douglas-fir. This conversion has brought with it increases in the significance of root disease and some bark beetles, such as Douglas-fir beetles and fir engraver beetles (*Scolytus ventralis)*. The extensive Douglas-fir beetle outbreak the northwestern portions of M333d (on and near the Idaho Panhandle National Forests) in 1998 and is evidence of this trend. Although the distributions of root pathogens have probably been little affected by the increase in abundance of host trees, the severity of the diseases have probably increased dramatically in habitats which were once occupied by white pine forests. Douglas-fir and grand fir were present in most of these forests in the 1935 era as a part of the mixture, but they were apparently only infrequently abundant enough to define the forest type. In our sample of M333d, 6.4 percent of hectares had been identified as having Douglas-fir and 2.5 percent as grand fir (in mixture with western redcedar or western hemlock) cover types in the 1935 era. By the 1975 era, Douglas-fir and grand fir cover types covered 10.7 percent and 14.1 percent of the hectares, respectively.

Suspended succession. On 28 percent of hectares, severe root disease effectively held stands in a state of suspended succession. This function, identified as "stalled structure," is one in which seedling/sapling stands of Douglas-fir, grand fir, or subalpine fir were seen to remain so for the 40-year interval of this analysis. In the context of rangeland succession, Laycock (1991) used "suspended stages of succession" to describe plant communities that remain almost unchanged in species composition for relatively long periods. In our case, the suspended stage of succession is also identified by an unchanging structure class in what would ordinarily be considered a short-term structure on such productive sites. This function (stalled structure with essentially unchanging cover type) was produced under what appear to be natural conditions. These features are common to root disease patches. Other, less obvious, cases of suspended succession were seen in the retention of early seral species on many sites (22 percent of hectares). Again, this was generally due to the actions of root pathogens and bark beetles, which kill mid- to late-seral tree species.

Table 7.2: Ecosection M333d: Influences of pathogens and insects from 1935 to 1975 eras.

Pathogen/Insect	Proportion of ha*	Primary Cover Effects (proportion)**	Primary Structure Effects (proportion)
White pine blister rust	.43	Increase climax (.76) Maintain early seral (.21)	No effect (.52) Toward immature (.29) Prevent closure (.16)
Root pathogens	.48	Increase climax (.7) Maintain early seral (.24)	Toward immature (.46) No effect (.30) Prevent closure (.21)
White pine blister rust and root disease combined	.30	Increase climax (.75) Maintain early seral (.21)	Toward immature (.44) No effect (.33) Prevent closure (.23)
Douglas-fir beetle	.04	Increase climax (.64) Increase early seral (.20) No effect (.15)	Prevent closure (.57) Toward immature (.28)
Mountain pine beetle, lodgepole pine	.03	Increase climax (.63)	Toward immature (.56) No effect (.29)
Bark beetles, ponderosa pine	.02	Increase climax (.64) Maintain early seral (.36)	Toward immature (.66) Prevent closure (.24)
Mountain pine beetle, white pine	.04	Increase climax (.81) Maintain early seral (.14) No effect (.04)	No effect (.50) Decrease density (.24) Prevent closure (.07)
Douglas-fir dwarf mistletoe	.02	Increase climax (.60) No effect (.29)	Prevent closure (.97)
Lodgepole pine dwarf mistletoe	<.01	Maintain early seral (1.0)	Prevent closure (1.0)
Western larch dwarf mistletoe	.01	Increase climax (.92)	Prevent closure (1.0)
Stem decays	.01	No effect (.50) Increase climax (.38)	Prevent closure (.82)
Spruce beetle	.02	No effect (.50) Increase climax (.49)	Toward immature (.72) Prevent closure (.15)
Spruce budworm	<.01	No effect (.59) Maintain early seral (.38)	Prevent closure (1.0)

*Proportion of hectares in M332a that are expected to be strongly influenced by the pathogen or insect.
**Of the hectares expected to be most affected by the pathogen or insect, the proportion likely to show each successional effect

Trends from 1935 to 1975 Eras: How Did We Get to 1975-era Conditions?

Most of the changes in forest conditions in our sample from 1935 to 1975 eras were strongly influenced by pathogens and insects. Their most important functions over this period were to push toward climax species composition and reduce or prevent canopy closure (Table 7.3). On

26 percent of hectares in M332a and 21 percent of hectares in M333d, where they had moderate to high probabilities, pathogens and insects effectively stalled structure development, maintaining forests in early structure classes for 40 years. This role was most evident on the most productive habitat types. A high percentage (62 percent in M332a and 58 percent in M333d) of pathways were identified as likely unique to those produced by pathogens and insects. As such, they represent some of the important ways in which pathogens and insects maintain ecological diversity. Stalled structure development is a good example of this type of pathway: in a 40-year time step, the polygon is seen to have remained in, or returned to, a seedling/sapling class.

Table 7.3: Trends in cover types and structure; 1935 to 1975 eras.

	Proportion (ha)	
Trends in Cover Type	**M332a**	**M333d**
Increase climax species composition	.52	.55
Species composition stable (no change)	.21	.10
Maintain early seral component/s	.20	.30
Increase proportion of early seral components	.07	.05
Trends In Structure		
Structure stable (no change)	.28	.06
Canopy closure prevented (low canopy density results)	.16	.16
Normal change to larger trees with nearly closed canopies	.17	.21
Largest trees die; move toward young, small tree classes	.18	.16
Structure stalled in young, small tree class	.12	.28
Large-tree structure; decrease in canopy density	.02	.01
Large-tree structure; increase in canopy density	.08	.12

White pine blister rust-influenced pathways were mostly unique to this agent. As an introduced pathogen, it has carved a unique niche in forests of ecosection M333d. The rapid transition of young, predominantly white pine stands to Douglas-fir, grand fir, and western redcedar is well-documented in this analysis. The subsequent loss of mature, closed-canopy western white pine successional stages has greatly altered the composition of much of northern Idaho and western Montana. Mountain pine beetle in western white pine once played an important role in the ecology of forests in M333d, and has shared the limelight with white pine blister rust since the early 1930s. In our sample of this ecosection, 1935-era white pine forest type in large-tree, closed canopy conditions all changed to other forest types or structure classes. Generally the changes were to more climax species compositions while remaining in, or returning to, large-tree, closed-canopy structures by the 1975 era. About 31 percent of the hectares in habitat group 5 (the largest group in M333d) that had white pine forest type and large, closed canopy structures had changed to pole-size or large-tree structures with low basal area, or to non-forest. In habitat type group 7, all polygons changed from white pine to other species, and 57 percent became pole-size stands or large-tree stands with low basal area.

Habitat type groups 2, 4, 5, and 7 were especially well-represented in the sample of M332a, and Douglas-fir forest type was particularly common in both the 1935-era and 1975-era

surveys, representing about 20 percent of the sample hectares in each time period. This was generally not because places that had a Douglas-fir forest type remained so, but mostly a result of areas moving into and out of Douglas-fir forest type at about the same rate. Most of the new Douglas-fir forest type came from polygons that previously had ponderosa pine or Douglas-fir/ponderosa pine mixed forest types, while most the migration out of Douglas-fir forest type was into either a cedar/Douglas-fir mix or various combinations that included subalpine fir. The overall result was a general movement toward more climax forest types. Both root disease and Douglas-fir beetle were important in moving forest types from Douglas-fir and Douglas-fir mixtures into late-seral or climax compositions.

CURRENT TRENDS: PROJECTING THE SAMPLE POLYGONS INTO THE FUTURE

If we assume that pathogens and insects will react in similar ways to a given forest condition in the second 40-year period as they did from 1935 to 1975 eras, and if we assume the sample represents polygons that remain unharvested and unburned from 1975 to 2015, then a rough estimate of current trends is possible. This estimate provides a glimpse into the probable future of the majority of land in ecosections M332a and M333d that will neither be harvested nor burned before the year 2015.

M332a: Pathogen and Insect Functions, 1975 to 2015

Based on the APIs in 1975 and the types of changes observed in polygon classes between 1935 and 1975 eras, root diseases and Douglas-fir beetle are expected to be the most significant influences from 1975 to 2015 (Table 7.4). Mountain pine beetle is expect to be much less common, dropping from 19 percent to 9 percent of hectares. Blister rust influence has declined with the loss of white pine to the disease and to mountain pine beetle attacks. Spruce beetle is expected to increase somewhat to about 6 percent of hectares. Although this number is small, the effects are typically concentrated on contiguous areas, so a number of locally-significant outbreaks are likely to occur. Stem decays are also expected to undergo a slight increase by 2015. As more forests enter later-seral and maturing tree classes, these diseases are expected to continue their increase.

Table 7.4: Expected trends: Influences of pathogens and insects in ecosection M332a from 1975 to 2015.

Pathogen/Insect	Proportion of ha*	Primary Cover Effect (proportion)**	Primary Structure Effect (proportion)
White pine blister rust	<.01		
Root pathogens	.43	Increase climax (.6) Maintain seral (.2)	Toward immature (.3) Prevent closure (.3) No effect (.3)
Douglas-fir beetle	.18	Increase climax (.6)	Prevent closure (.4) No effect (.3)
Mountain pine beetle, lodgepole pine	.09	Increase climax (.9)	No effect (.7)
Bark beetles, ponderosa pine	.05	Increase climax (.8)	Toward immature (.5) Prevent closure (.3)

Mountain pine beetle, white pine	<.01		
Douglas-fir dwarf mistletoe	.04	No effect (.5) Maintain seral (.4)	Prevent closure (>.9)
Lodgepole pine dwarf mistletoe	<.01		
Western larch dwarf mistletoe	<.01		
Stem decays	.04	No effect (.5) Maintain seral (.4)	Prevent closure (.9)
Spruce beetle	.06	Increase climax (.9)	No effect (.9)
Spruce budworm	.03	No effect (.6)	Prevent closure (>.9)

*Proportion of hectares in M332a that are expected to be strongly influenced by the pathogen or insect.
**Of the hectares expected to be most affected by the pathogen or insect, the proportion likely to show each successional effect.

There are a couple of changes in function trends expected in polygons with the greatest influences from pathogens and insects (Figure 7.1). The portion of the sample area on which pathogens and/or insects cause an increase in early-seral species is expected to rise from about 9 percent in the first 40 years to closer to 16 percent of hectares from 1975 to 2015. Also, because of the greater proportion of the sample area that already has climax or near-climax species composition, the pathogens and insects are expected to have less influence on cover type changes in the second 40 years, with 39 percent remaining unchanged (compared to 20 percent from 1935 to 1975 eras). With the changes toward more climax composition, the trend toward larger trees is expected to be more pronounced in the second 40 years as fewer stands are retained in the small tree classes. A decline from 46 percent to 28 percent of hectares exhibiting these functions is expected (Figure 7.2). Relatively open canopies are expected in much of the large- tree classes, caused by continued pathogen- and insect-caused mortality. This function is expected to increase in frequency from 21 percent in the period from 1935 to eras 1975 to 40 percent from 1975 to 2015.

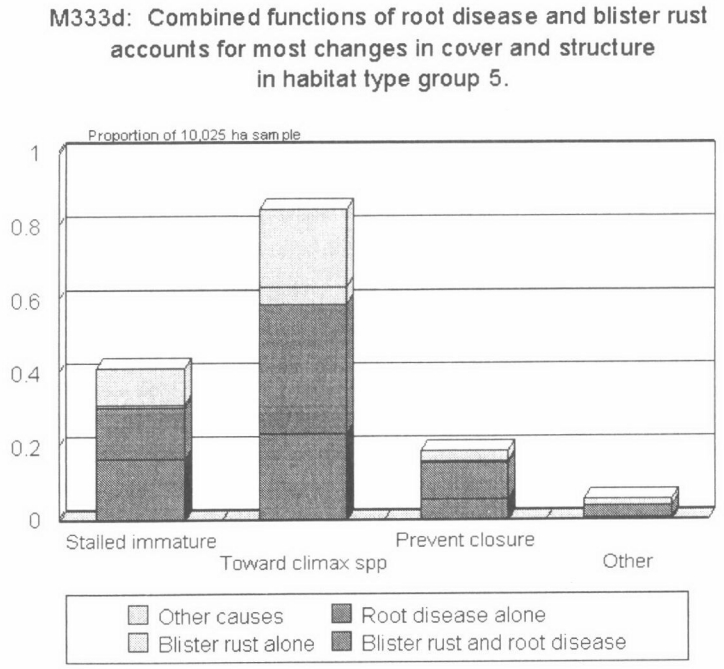

Figure 7.1: Functions of pathogens and insects in highly affected polygons: cover type changes for 1935 to 1975 eras and for 1975 to 2015, M332a.

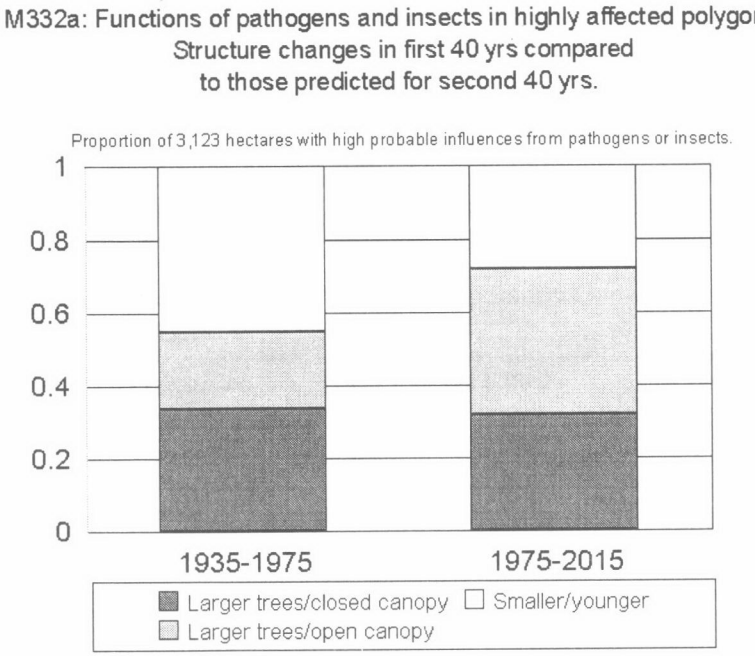

Figure 7.2: Functions of pathogens and insects in highly affected polygons: structure class changes for 1935 to 1975 eras and for 1975 to 2015, M332a.

Trends in M332a, 1975 to 2015

From 1935 to 1975 eras, 10 percent of the sample hectares remained in the same cover type and structure classes. On the basis of the polygon classes in the 1975 sample, 20 percent are expected to remain in the same cover type and structure class through the year 2015. These polygons were classified as climax or near-climax species composition, with large trees and closed canopy structure in 1975. The next largest category (8 percent of hectares) are polygons that are expected to remain in climax or near climax species composition while canopy closure is prevented (ending in structure class 4 in 2015). In the previous 40 years, only 3 percent of the sample hectares underwent this type of change, primarily because so few polygons were classified as late-seral cover types.

Overall, 45 percent of the 1975 sample is expected to remain in late-seral or climax cover types and another 24 percent are expected to continue to increase the relative proportions of late seral species sufficiently to classify as a later-seral cover type (Table 7.5). Early seral species are expected to be maintained as the cover type on about 31 percent of hectares. This represents the continuation of a significant trend toward increasingly uniform species composition in the forests, signaling a loss of beta diversity through the loss of early-seral forests.

Table 7.5: Expected trends in cover types and structure in M332a: 1975 to 2015.

TRENDS	PROPORTION (ha)
Trends in cover type	
Increase climax species composition	.24
Species composition stable (no change expected)	.45
Maintain early seral component/s	.19
Increase proportion of early seral components	.12
Trends in Structure Type	
Structure stable (no change expected)	.35
Canopy closure prevented (low canopy density results)	.18
Normal change to larger trees with nearly closed canopies	.12
Largest trees die; move toward young, small tree classes	.10
Structure stalled in young, small tree class	.10
Large-tree structure; decrease in canopy density	.08
Large-tree structure; increase in canopy density	.05

Approximately half of the hectares are expected to remain in the same structure–generally a mature, well-stocked condition–or to grow into this structure class by 2015. One fourth is expected to be in large-tree structure with pathogens and insects preventing the canopy from closing. About one fifth of hectares is expected to remained stalled in early structure classes (seedling/sapling or pole) for another 40 years or to regress from larger tree structures to small/young tree structures. This proportion is similar to that observed from 1935 to 1975 eras.

Looking only at habitat type groups (groups 3, 4, and 5) in which trees are expected to reach large-tree sizes, the trend is even more pronounced. Of the hectares that were in seedling/sapling or pole structure classes in 1975, somewhat more area is expected to remained stalled (33 percent) through the year 2015 than that expected to progress to large-tree, closed-canopy structures (26 percent).

The converse was true from 1935 to 1975 eras in which 25 percent of these small-tree structure classes remained stalled and 50 percent progressed to large-tree, closed-canopy structures. The stands that stalled from 1935 to 1975 eras are more likely to continue to stall for another 40 years (53 percent) than are those that did not remain seedling/sapling or pole stands throughout the previous 40 years (17 percent).

The net result of these changes would be a continued increase in the relative proportions of grand fir, subalpine fir, and cedar/grand fir cover types (Figure 7.3). After a fairly dramatic increase from 1935 to 1975 eras, Douglas-fir cover type is expected to decline. This will likely result from root disease and Douglas-fir beetle activity. A continued decline in proportions of ponderosa pine and lodgepole pine cover types is expected as well.

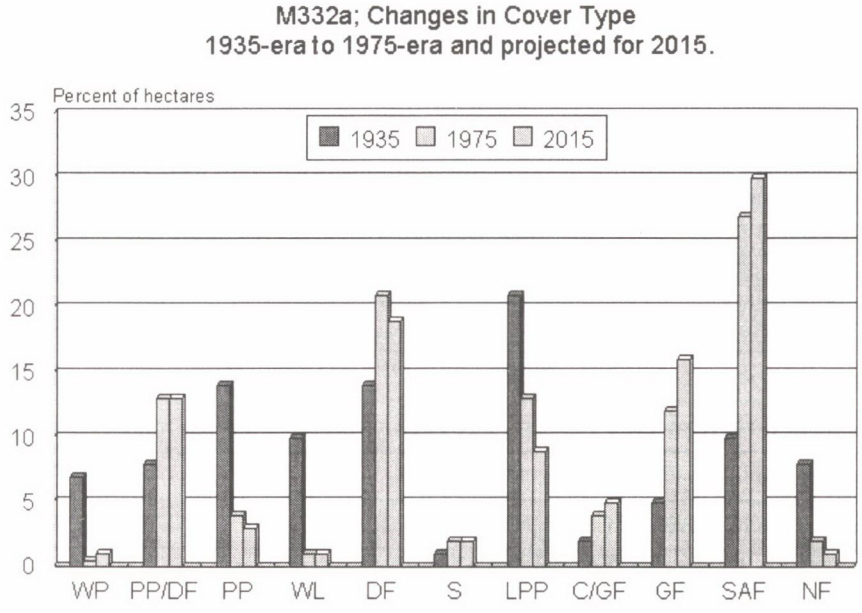

Figure 7.3: Changes in cover type, 1935 to 1975, and projected for 2015, M332a.

Structure class 0 (non-stocked) is expected to continue to be reduced unless regeneration harvests or fires increase. After a small increase in structure class 1 (seedling/sapling) in the first period, a decline is predicted as forests grow into class 2, 3, or 4. Structure class 2 (pole, moderately to well-stocked) may decline somewhat as larger-tree classes are achieved. Structure class 3 (large-tree, closed canopy) is expected to continue to increase somewhat. Structure class 4 (large-tree, broken canopy), which had declined somewhat from 1935 to 1975 eras, is expected

to increase for the next few decades as stands in structure classes 2 and 3 are affected by pathogens and insects that prevent the development of closed canopies (Figure 7.4).

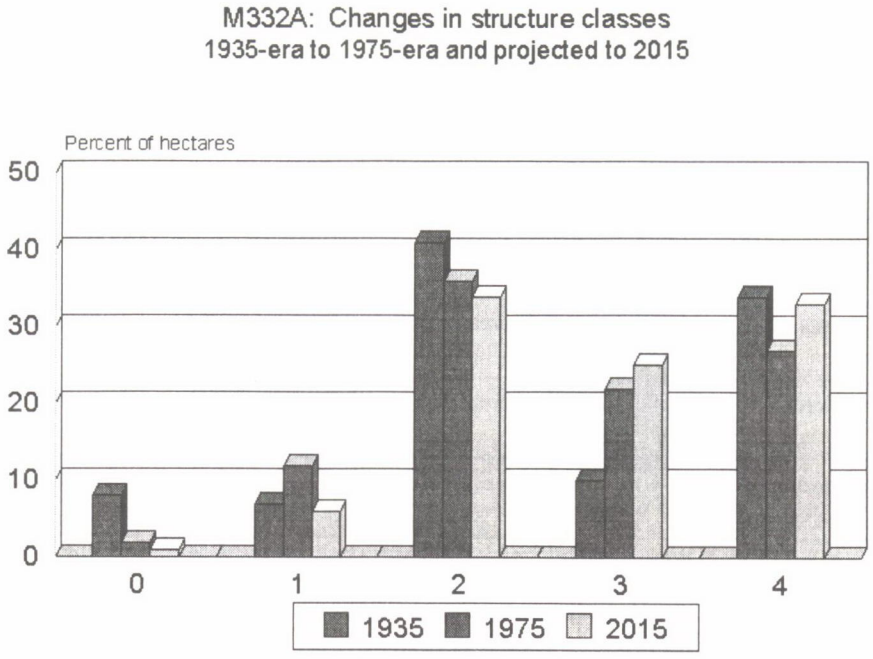

Figure 7.4: Changes in structure classes, 1935 to 1975, and projected for 2015, M332a.

M333d: Pathogen and Insect Functions, 1975 to 2015

Based on the APIs from 1975-era data and the types of changes observed in polygon classes represented in 1935-era to 1975-era transitions, blister rust and root diseases are expected to continue to be the most significant influences from 1975 to 2015 (Table 7.6). In addition, Douglas-fir beetle is expected to increase dramatically. Mountain pine beetle in lodgepole pine is also expected to increase substantially in the next decades. Douglas-fir dwarf mistletoe and stem decays are expected to expand and intensify during these decades as well. Mountain pine beetle in ponderosa pine is expected to increase for a while as young pines reach maturity. A small increase is also expected in larch dwarf mistletoe as the small remaining larch component continues to mature. Western spruce budworm is also expected to increase as the Douglas-fir, grand fir and subalpine fir hosts grow increasingly multi-storied. This is particularly likely on and near the Clearwater and Lolo National Forests, where outbreaks have occurred in the past.

Table 7.6: Expected trends: Influences of pathogens and insects in ecosection M333d from 1975 to 2015.

Pathogen/Insect	Proportion of ha*	Primary Cover Effect (proportion)**	Primary Structure Effect (proportion)
White pine blister rust	.35	Increase climax (.6)	No effect (.4) Prevent closure (.4)
Root pathogens	.66	Increase climax (.6)	Toward immature (.4) Prevent closure (.4)
Douglas-fir beetle	.18	No effect (.5) Increase climax (.40)	Prevent closure (.6) Toward immature (.3)
Mountain pine beetle, lodgepole pine	.12	Increase climax (.7)	Toward immature (.6)
Bark beetles, ponderosa pine	.08	Increase climax (.9)	Toward immature (.5) Prevent closure (.5)
Mountain pine beetle, white pine	.03	No effect (.7)	Prevent closure (.9)
Douglas-fir dwarf mistletoe	.19	No effect (.6)	Prevent closure (>.9)
Lodgepole pine dwarf mistletoe	>.01	Maintain seral (>.9)	Prevent closure (>.9)
Western larch dwarf mistletoe	.03	Increase climax (>.9)	Prevent closure (>.9)
Stem decays	.08	No effect (.6)	Prevent closure (.9)
Spruce beetle	.02	No effect (.7)	Prevent closure (.5) Toward immature (.4)
Spruce budworm	.04	No effect (>.9)	Prevent closure (>.9)

*Proportion of hectares in M333d that are expected to be strongly influenced by the pathogen or insect.
**Of the hectares expected to be most affected by the pathogen or insect, the proportion likely to show each successional effect.

The overall effect of pathogens and insects in the most-affected polygons–those with moderate to high influences from at least one pathogen or insect–appears to be surprisingly stable. In comparing the major functions from the first 40 years (1935 to 1975) to the second 40 years (1975 to 2015), the proportional changes in trend are relatively minor. In the first period, 37 percent of hectares were seen to be stalled in young tree structures or to regress from large-tree to small-tree structures. For the second period, 37 percent of hectares are expected to follow this trend (Figure 7.5). A slightly smaller proportion, 40 percent compared to 44 percent are expected to move into or remain in the large-tree, closed canopy structure class. Similarly, the same proportion of hectares is predicted to retain or increase seral species composition as did in the first 40 years (34 percent) (Figure 7.6). These are a fairly remarkable outcomes considering there have been great changes in tree species composition and in the relative importance of the various pathogens and insects. It appears that much of the role played by white pine blister rust in the first 40 years will be assumed, in the broad sense, by root pathogens and bark beetles.

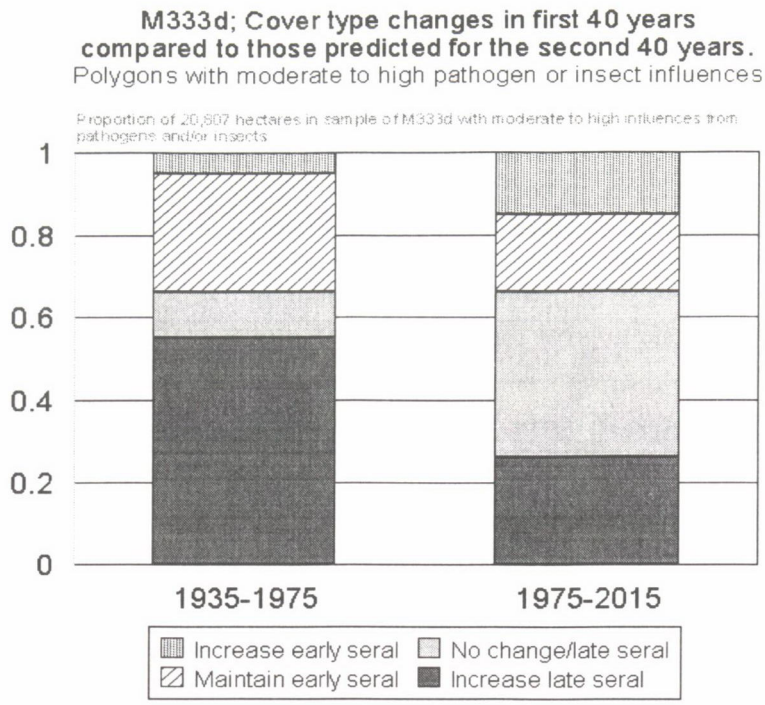

Figure 7.5: Changes in cover type, M333d.

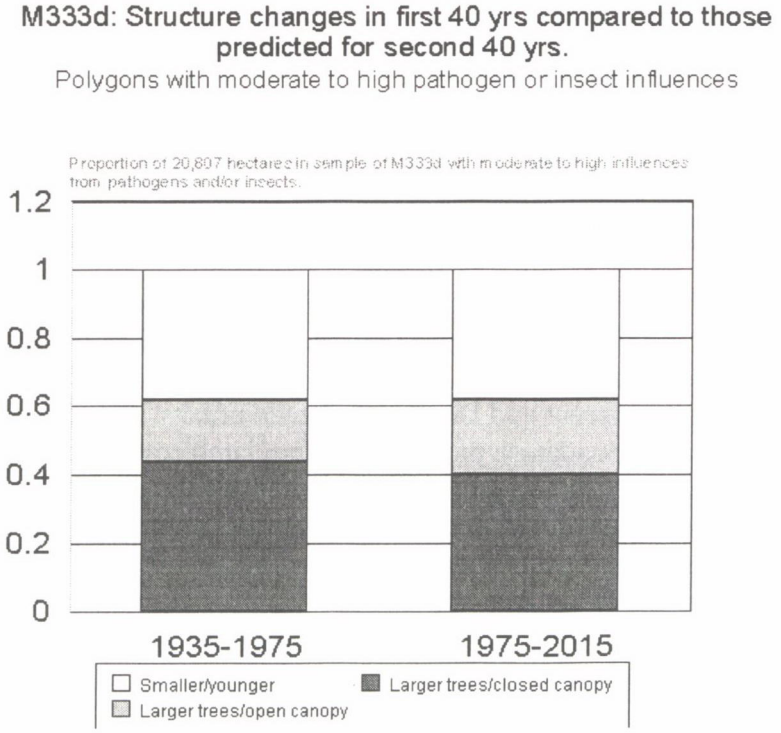

Figure 7.6: Changes in structure classes, M333d.

Trends in M333d, 1975 to 2015

In M333d, cover trends in species composition are toward more stability, with approximately 80 percent of stands either progressing toward more climax species or remaining stable in largely climax species composition (Table 7.7). Less than 20 percent of hectares are expected to maintain early-seral species compositions. The trends in structure are striking in this ecosection, however, with about 65 percent of hectares expected to have low canopy conditions, remain stalled in small, young tree structures for the 40-year period or move into small, young-tree structures by 2015 as a result of pathogen and insect activities. Only about one third of stands are expected to continue to grow into a larger-tree, closed-canopy structure or to remain stable in these structures.

Table 7.7: Expected trends in cover types and structure in M333d, 1975 to 2015.

TRENDS	PROPORTION (ha)
Trends in cover type	
Increase climax species composition	.57
Species composition stable (no change expected)	.24
Maintain early seral component/s	.15
Increase proportion of early seral components	.03
Trends in Structure	
Canopy closure prevented (low canopy density results)	.29
Normal change to larger trees with nearly closed canopies	.22
Structure stalled in young, small tree class	.21
Largest trees die; move toward young, small tree classes	.13
Large-tree structure; increase in canopy density	.10
Structure stable (no change expected)	.04

The net result of these changes would be a continued increase in the relative proportions of grand fir, subalpine fir, wester hemlock/grand fir, and cedar/grand fir cover types (Figure 7.7). Also expected is a fairly dramatic decline in Douglas-fir: back to about 1935-era levels. This would likely result from root disease and Douglas-fir beetle effects. A continued decline in proportions of western white pine, ponderosa pine, and western larch cover types is expected, though less dramatic than the decline of these species over the first 40-year period. Lodgepole pine increased in the first 40-year period, but as it reaches maturity, mountain pine beetle depredations are expected to cause a significant decline in the period from 1975 to 2015. Recent mountain pine beetle impacts on the Avery and Superior Ranger Districts are probably part of this predicted trend.

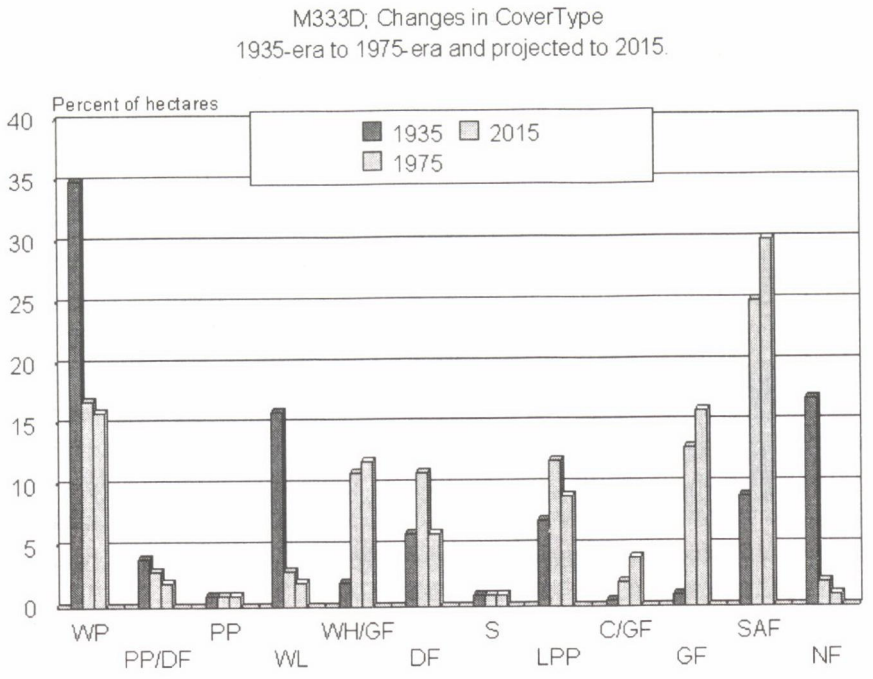

Figure 7.7: Changes in cover type, 1935 to 1975, and projected for 2015, M333d

Structure classes 0 (non-stocked) and 1 (seedling/sapling) are expected to continue to disappear. Structure class 2 (pole, moderately to well-stocked) may decline somewhat as larger tree classes are achieved. Structure class 3 (large-tree, closed-canopy) is expected to continue to increase somewhat. Structure class 4 (large-tree, low-density, and broken canopy), which had declined fairly dramatically from 1935 to 1975 eras, is expected to increase for the next few decades as stands in structure classes 2 and 3 are affected by root disease and bark beetle outbreaks (Figure 7.8).

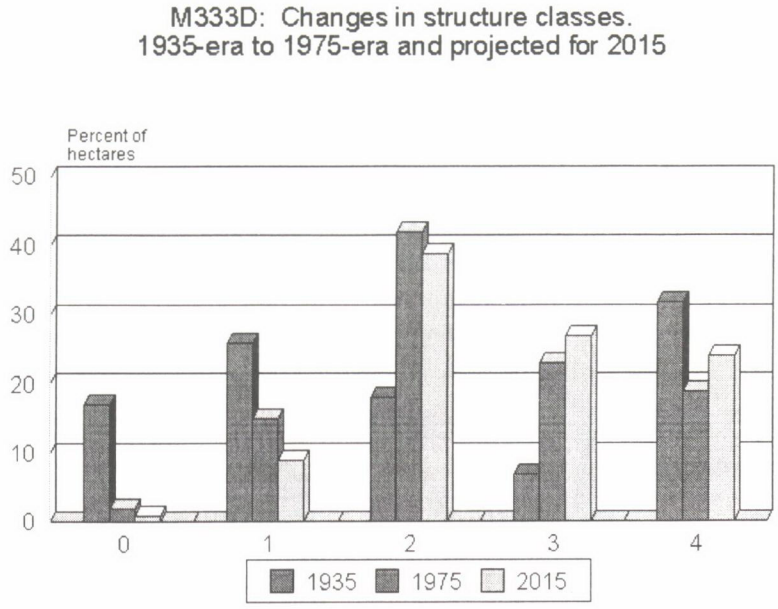

Figure 7.8: Changes in structure classes, M333d.

RELATIONSHIP TO OTHER LOCAL ASSESSMENTS AND TOOLS

Hazard and Risk-rating Procedures

Functions of pathogens and insects in forests can be divided into two parts: 1) the action, such as killing trees, decaying heartwood, or reducing growth; and 2) the outcome, such as changing species composition of a stand or causing a change from a mature, closed canopy structure to a pole-size, low-density structure.

Among the first steps in this analysis was the development of a system to assess the relative probability of an insect or pathogen *action* occurring in a stand. The results were Action Probability Indices (API) for each of the 12 pathogens and insects included in the study. The API is essentially a system of rating stands for risk of pathogen or insect activities sufficient to alter the course or timing of succession. It hardly seems appropriate to label this activity a "risk," however, considering that many of the outcomes could be considered positive effects. Among these, commonly, was the retention of early seral species that otherwise may have been overgrown by the often less-desirable, later-seral species. The index simply reflects the relative probability of a significant action on the part of a given pathogen or insect, whether the outcome is desirable or not.

Most risk-rating procedures are designed to classify stands according to relative probability of "serious stand damage" (Scott and Schmitt 1995) should a sufficient, local population of insects or pathogens be available. The objective of risk rating usually is to set priorities for timber salvage or stand management based on the risk of mortality or growth loss from a particular agent. Increasing risk levels also have been interpreted to signal a deterioration of forest conditions. In the case of forest insects or diseases, managers have traditionally regarded high risk of an outbreak as high priority for treatment. Although the objectives of the APIs used in the

present analysis differ somewhat from risk rating systems, the systems are, nonetheless, very similar in structure (with the exception of root disease severity rating). In fact, the research basis for most of APIs often were the same as those used for the UPEST insect and disease risk calculator developed for the Blue Mountains of Oregon (Ager et al. 1995) and the insect and disease hazard rating system used in the Upper Columbia River Basin project (Hessburg et al.1996, unpublished). These are both locally well-known systems for calculating risks of multiple insects and pathogens.

Risk or hazard rating systems utilize stand and/or site characteristics to classify stands according to their relative degree of suitability for a given pathogen or insect. In this regard, the API values (except root disease severity) are similar to hazard or risk-rating values. The present analysis employed a number of published risk-rating systems, with some modification. For example, the mountain pine beetle in lodgepole pine stand susceptibility rating system developed by Amman et al. (1977) was modified by Randall for use in this analysis (see Methods; Part 2). The index she developed was designed to reflect relative probability of effects from mountain pine beetle that would alter the course or timing of forest succession. Validation of this modified index is seen in detection of successional outcomes that were consistent with mountain pine beetle effects in stands. This, then, is the greatest difference between most risk rating projects and the present analysis. The APIs for polygon classes were compared to the successional changes observed in each class over the 40-year period (1935 to 1975 eras) as a means to assign most probable cause to the resulting successional pathways and to validate the notion that risk leads to some predictable type and frequency of change. This interpretation of successional effect from single and combinations of pathogens and insects was the primary focus of the analysis.

Landscape and Forest Planning

Probability indices for pathogens and insects

This analysis was intended to provide a means to study and assess the functions of tree pathogens and insects in forest ecosystems, and to assess past and current trends in those functions. We have reported herein on both aspects of this project. The extensive database which we amassed for this analysis also was designed to provide information useful for forest and landscape planning. The action probability indices reflect the relative probability of significant activity for each of the studied pathogens and insects. These can be calculated individually for stands with standard (R1-Edit) stand-level data or they can be applied as average, range, or frequency statistics by polygon class. Polygons can be classified in any of a number of ways, with the disease and insect statistics calculated according the specified classification scheme. This approach was taken because there is currently little consistency among National Forests and other forest land owners in the site- and stand-classification schemes utilized in local planning efforts. There are ongoing efforts within the US Forest Service and other groups to produce a broadly accepted vegetation classification system. These efforts are of critical importance the efficiency and across-border compatibility of forest and landscape planning efforts.

Interpreting the indices: alternatives for portraying significance and trends

The APIs, like risk indices, are subject to interpretation. High index values refer only to the relative susceptibility of stands to effects from the pathogen or insect (or a combination of agents). To understand the relative probability of an outbreak or its probable outcome, should it occur, results of the successional analysis by polygon classes should be consulted. Successional

effects associated with each of the pathogen/insect/polygon class combinations are applicable to forest and landscape-level planning. They provide a means to predict trends in vegetation cover and structure as well as pathogen and insect APIs for the majority of areas on most National Forests that are not expected to be harvested or burned in the next few decades.

Where it is more desirable to base assessment on polygon classes, such as in the case of remote-sensed data, the statistics representative of pathogen and insect activities in polygon classes will provide general trends according to the abundance and distribution of polygon classes within an analysis area. The statistics from each of the ecoregion ecosections examined in our analysis represent the range and frequency of pathogen and insect APIs. The transition analysis for each polygon class provides relevant trends for each class within the ecoregions. For landscape and National Forest-level analyses, geographic information system technology is used to assign the ecoregion ecosection identity to polygons and apply the appropriate statistics to each polygon.

Stand and landscape models

The use of geographically explicit data from two time periods resulted in generation of considerable data on transitions during the 40-year analysis period. These data represent a large range of conditions within each of the major ecoregion ecosections in the Northern Region, and may represent the first substantial database to be used in succession modeling. Most, perhaps all, landscape models currently in use in the Northern Region are based on limited data, relying heavily on professional judgement for succession pathways and probabilities. As a substantial effort to document successional changes, data from this analysis can be a start toward validation of existing landscape models such as CRBSUM (Keane et al.1996), the primary vegetation model used in the Columbia River Basin analysis, and SIMPPLLE (Chew 1995), a stand-based succession model demonstrated in the Bitterroot Ecosystem Management Demonstration Project and under development for other areas in the Northern Region.

The successional pathways and probabilities derived from the present analysis were used to calibrate the North Idaho variant of the Forest Vegetation Simulation (FVS) model (Stage 1973, Wykoff et al. 1982) for unharvested and unburned stands. The Dwarf Mistletoe Impact model (Chen et al. 1993, Taylor 1995) and the Western Root Disease model (Stage et al.1990, Beukema et al. 1995) of FVS are used in conjunction with the base FVS (growth and regeneration model) for these projections of the 1975-era stand data used in the present analysis. Using these FVS capabilities, we projected stands simulating the effects of dwarf mistletoes, root pathogens, bark beetles, and white pine blister rust. Most landscape models have annual or decade time steps rather than the 40-year time step represented in our analysis. The 10-year time steps resulting from the calibrated FVS outputs can provide a reasonable prediction of changes during the intervening years.

The outcomes from these 10-year intervals from FVS projections were then used to construct arrays of polygon classes, successional pathways and decadal transition probabilities for each ecoregion ecosection. Efforts are underway, in collaboration with the Flathead National Forest, to enter these data into the Vegetation Dynamics Development Tool (VDDT) (Beukema and Kurz 1995), which will allow us to compare the outcomes with those of the pathogen- and insect-designated pathways in the CRBSUM model. This process has constituted a significant project in itself, and will be reported elsewhere. However, FVS users in the Northern Region may want to note that we can now provide additional tools to enhance their FVS projections. Files of "addkeys," modifiers for the Western Root Disease and Dwarf Mistletoe Impact models,

are now available for improving the performance of these models based on the habitat type and initial root disease severity of projected stands.

General ecological and management implications

Unlike the outcome of most fire-induced changes, the most significant functions of pathogens and insects result in increasing the proportion of climax tree species in forests. This outcome may be considered undesirable in most situations in ecosections M332a and M333d where low proportions of early seral species such as pine and western larch are already a concern. In some situations, however, the pathogens and insects do favor the relatively resistant early seral tree species by killing Douglas-fir and grand fir, often later-seral or climax species on these sites. This function is probably important in habitat type groups 2, 3, and 7, in particular. Ponderosa pine, western larch, and lodgepole pine are the main beneficiaries of this type of function.

Pathogens and insects also function broadly to reduce stand density and prevent canopy closure. Although this can translate to heavy impacts on timber production, the multi-storied structure that generally results when canopy is reduced may be viewed by wildlife biologists and the viewing public as a desirable stand trait.

Recruitment and long-term retention of old growth, by most current definitions, may be difficult or impossible to achieve on many sites and with some tree species. In most cases, this is not because of unusual or unexpected insect or pathogen activities, but rather is a matter of course in natural succession where insects and pathogens respond to agreeable stand or site conditions. A most unfortunate exception to this are old growth western white pine forests, which were devastated, directly or indirectly, by the exotic pathogen, *Cronarium ribicola*, the cause of white pine blister rust. Recovery of the white pine forest type from this disease is unlikely, leaving the future of these ecosystems uncertain. Worldwide trade brings to our seaports continual threats of additional exotic introductions that have the potential for similarly devastating effects. It is important not to underestimate the ecological importance of existing and potential exotic introductions.

The activities of pathogens and insects occur to some degree in all stands, on all acres of the forest, each year. Most of the effects are cumulative over the course of forest development and throughout the process of forest succession. As such, there are limited opportunities to substantially alter the functions of pathogens and insects. Nearly all successful manipulation of pathogen or insect activities happens through vegetation management: altering the condition of the vegetation alters the opportunities for vegetation-dependent pathogens and insects.

With foresight, careful analysis of trends, and planning accordingly, we can maximize our effectiveness in vegetation management. The most obvious outbreaks of diseases and insects are not necessarily the most damaging from an ecological standpoint. It is important to focus on the outcomes of pathogen and insect actions rather than the pathogens or insects themselves if we are to identify the best times and places to concentrate our management efforts. Processes developed through this project can be employed to generate more meaningful forest plans, to analyze alternative actions, and to more accurately communicate those alternatives to the various publics served by private and public forest managers

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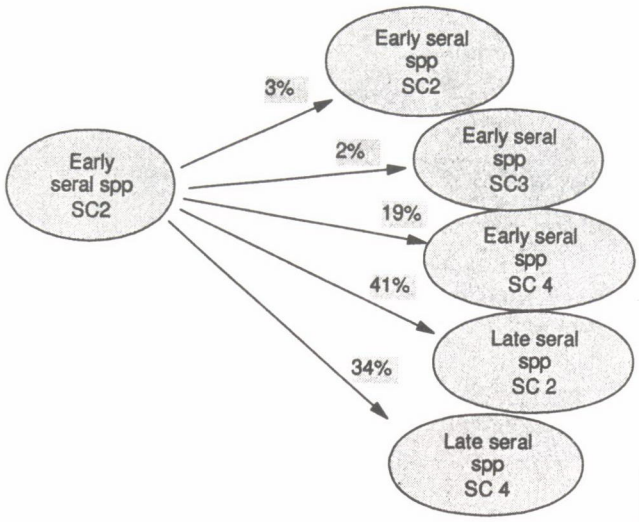
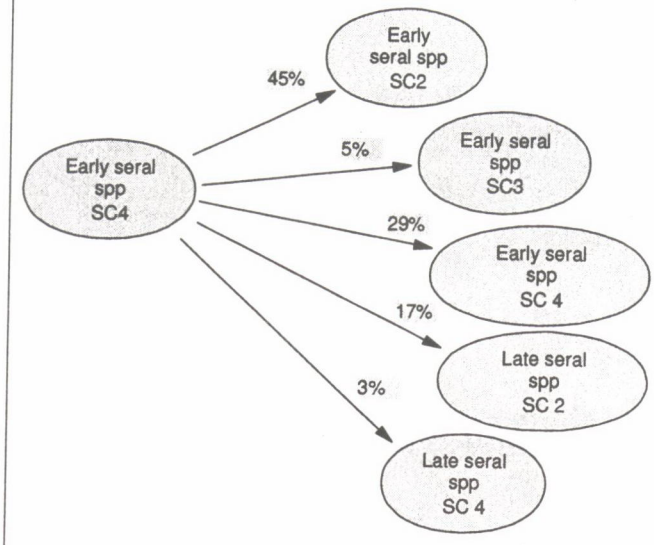
APPENDIX A: SUCCESSIONAL PATHWAYS FOR HABITAT TYPES WITH MODERATE TO HIGH ROOT DISEASE INFLUENCE

M332a, HT 2
Pathways from ponderosa pine or ponderosa pine/Douglas-fir cover type, in pole structure class.
Percent of hectares; 1935 -1975.



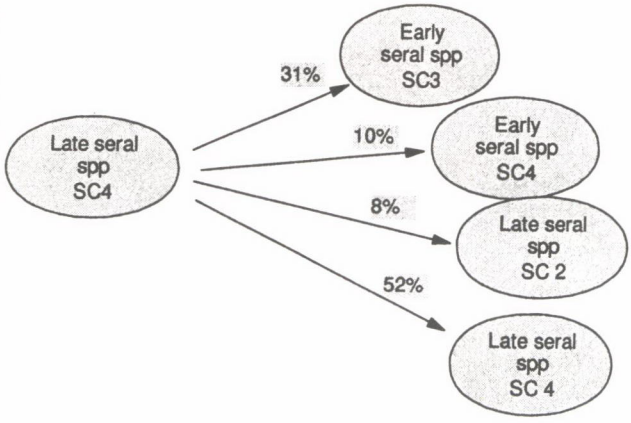
Early-seral spp. are generally ponderosa pine mixed with Douglas-fir, Late-seral spp. are generally Douglas fir, some grand fir.

M332a, HT 2:
Pathways from ponderosa pine or ponderosa pine/Douglas-fir cover type, large-tree, low density structure class.
Percent of hectares, 1935 - 1975.



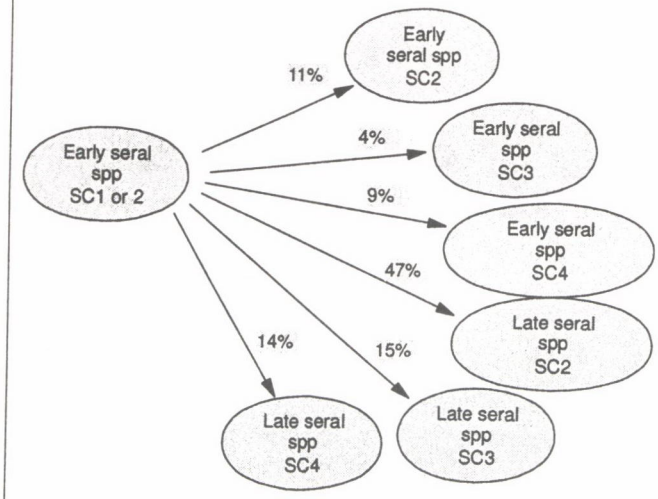
Early-seral spp. are generally ponderosa pine mixed with Douglas-fir, Late-seral spp. are generally Douglas-fir, some grand fir.

M332a, HT 2:
Pathways from Douglas-fir cover type, in large-tree, low density structure class.
Percent of hectares, 1935 - 1975.



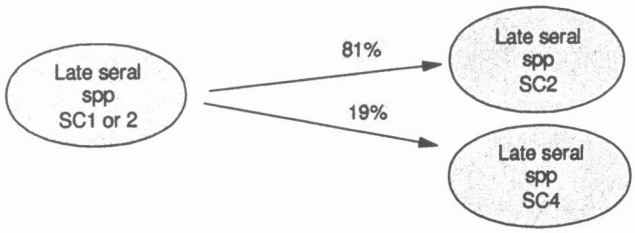
Early-seral spp. are generally ponderosa pine mixed with Douglas-fir, Late-seral spp. are generally Douglas-fir, some grand fir.

M333d, HT 2:
Pathways from ponderosa pine or ponserosa pine/Douglas-fir cover type, in seedling/sapling and pole structure classes.
Percent of hectares, 1935 - 1975.



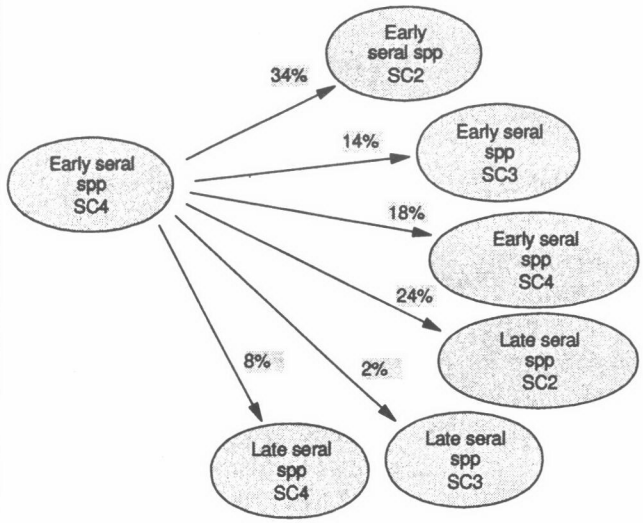
Early-seral spp. are generally ponderosa pine mixed with Douglas-fir, Late-seral spp. are generally Douglas-fir, some grand fir.

M333d, HT 2:
Pathways from Douglas-fir cover type,
in seedling/sapling and pole structure classes.
Percent of hectares,1935 to 1975.



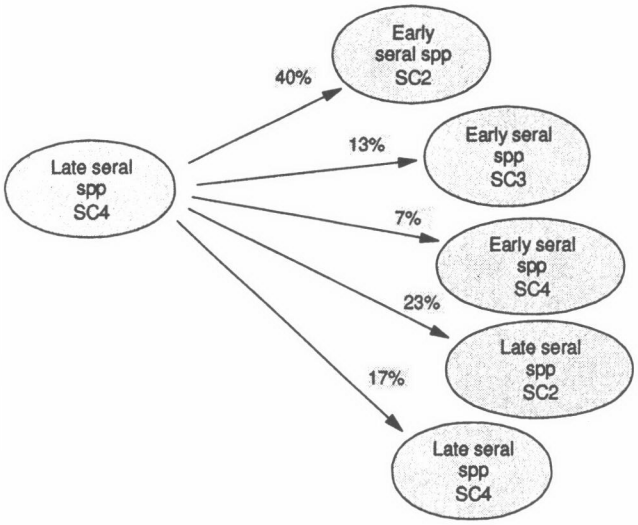
Early-seral spp. are generally ponderosa pine mixed with Douglas-fir,
Late-seral spp. are generally Douglas-fir, some grand fir.

M333d, HT 2:
Pathways from ponderosa pine or
ponderosa pine/Douglas-fir cover type,
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



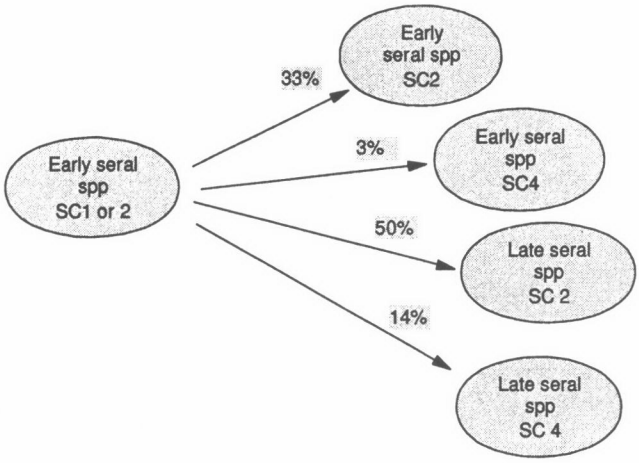
Early-seral spp. are generally ponderosa pine mixed with Douglas-fir,
Late-seral spp. are generally Douglas-fir, some grand fir.

M333d,HT 2:
Pathways from Douglas-fir cover type,
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



Early-seral spp. are generally ponderosa pine mixed with Douglas-fir,
Late-seral spp. are generally Douglas-fir, some grand fir.

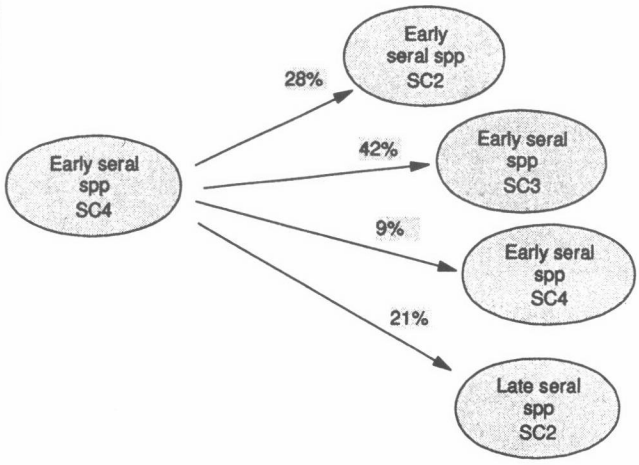
M333d, HT 3:
Pathways from pine and larch cover type,
in seedling/sapling or pole structure classes.
Percent of hectares, 1935 to 1975.



Early-seral spp. are generally mixtures with pines or larch,
Late-seral spp. are generally Douglas-fir and grand fir.

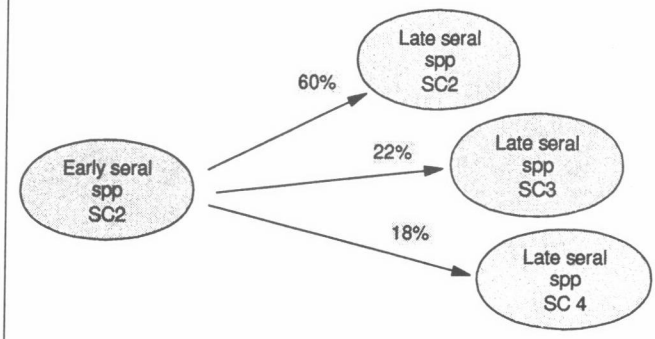
Appendix A: Successional Pathways with Moderate to High Root Disease Influence

M333d, HT 3:
Pathways from pine and larch cover type
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



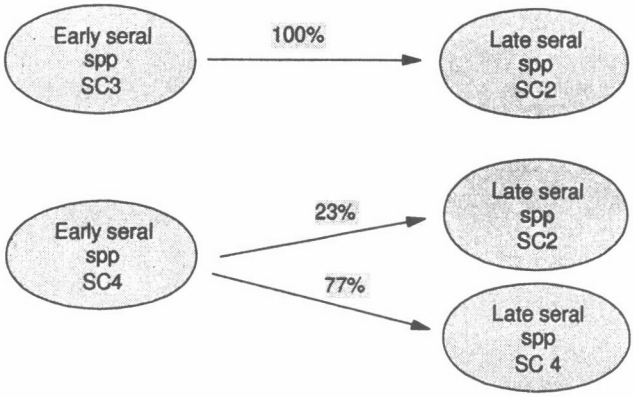
Early-seral spp. are generally mixtures with pines or larch,
Late-seral spp. are generally Douglas-fir and grand fir.

M332a, HT 4:
Pathways from pine and larch cover type,
in pole structure class.
Percent of hectares, 1935 to 1975.



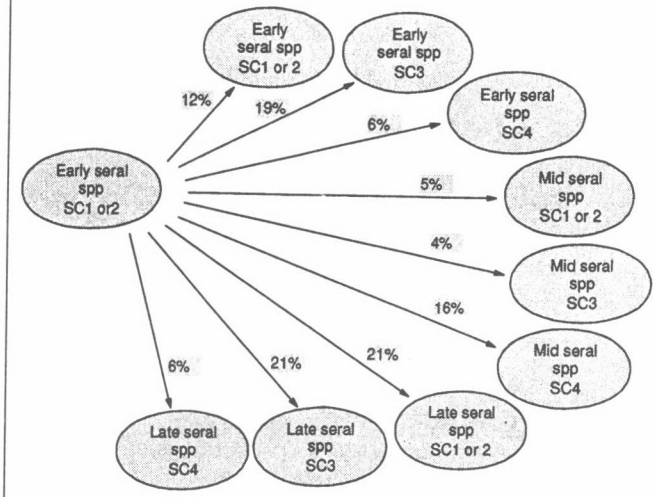
Early-seral spp. are generally mixtures with pines or larch,
Late-seral spp. are generally Douglas-fir and grand fir.

M332a, HT 4:
Pathways from pine and larch cover type,
in large tree structure classes.
Percent of hectares, 1935 to 1975.



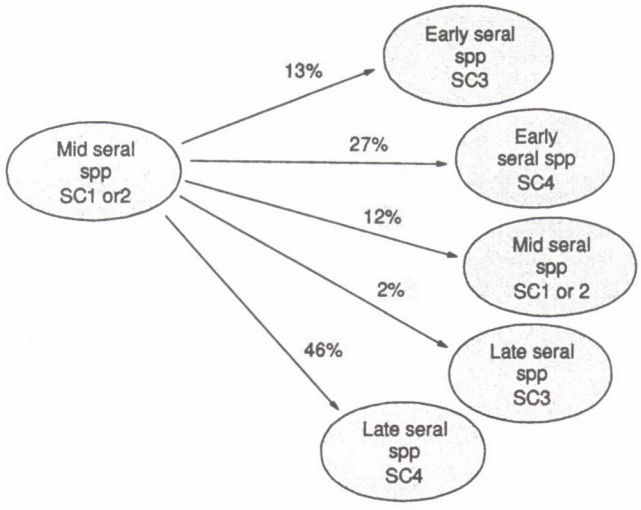
Early-seral spp. are generally mixtures with pines or larch,
Late-seral spp. are generally Douglas fir and grand fir.

M333d, HT 4:
Pathways from pines and larch cover type,
in seedling/sapling and pole structure classes.
Percent of hectares, 1935 to 1975.



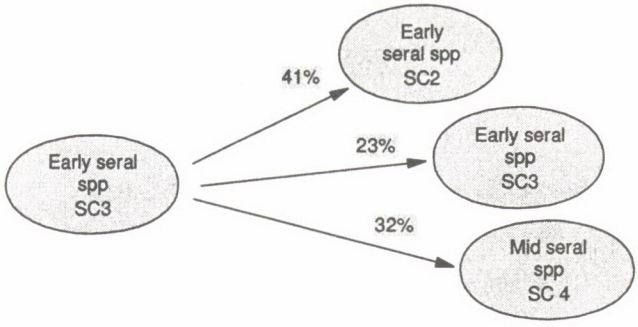
Early-seral spp. are mixtures with pine or larch,
Mid-seral spp. are heavy to Douglas-fir,
Late-seral spp. are heavy to grand fir.

M333d, HT 4:
Pathways from pines and larch cover type,
in seedling/sapling and pole structure classes.
Percent of hectares, 1935 to 1975.



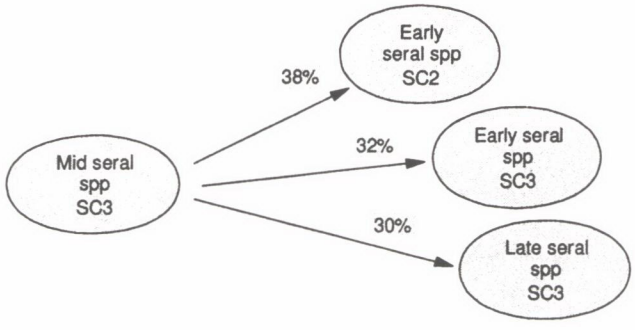
Early-seral spp. are mixtures with pine or larch,
Mid-seral spp. are heavy to Douglas-fir,
Late-seral spp. are heavy to grand fir.

M333d, HT 4:
Pathways from pine and larch cover type
in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



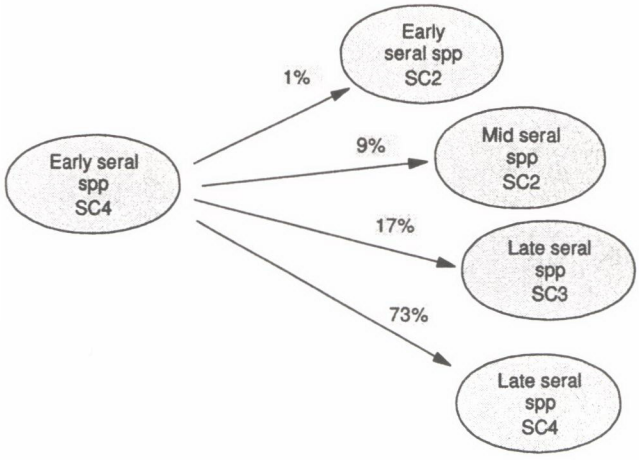
Early-seral spp. are mixtures with pines or larch,
Mid-seral spp. are heavy to Douglas-fir

M333d, HT 4:
Pathways from Douglas-fir cover type,
in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



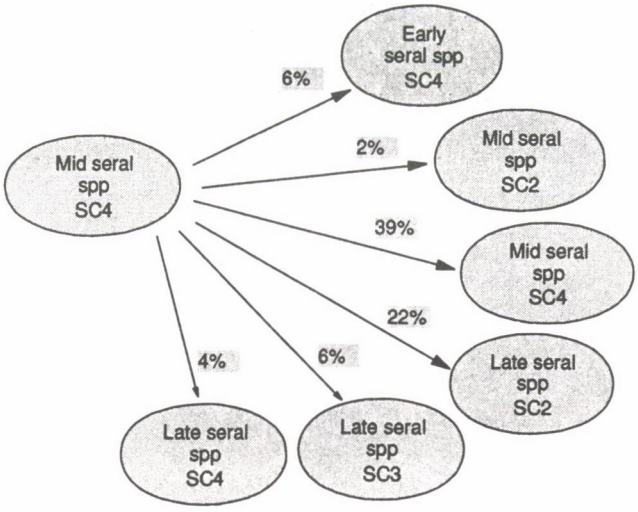
Early-seral spp. are mixtures with pines or larch,
Mid-seral spp. are heavy to Douglas-fir,
Late-seral spp. are heavy to grand fir.

M333d, HT 4:
Pathways from white pine and larch cover type
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



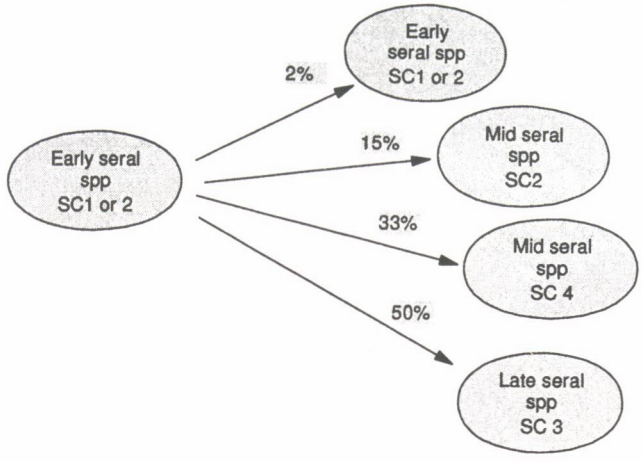
Early-seral spp. are white pine and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir,
Late-seral spp. are largely grand fir.

M333d, HT 4:
Pathways from Douglas-fir/grand fir cover type
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



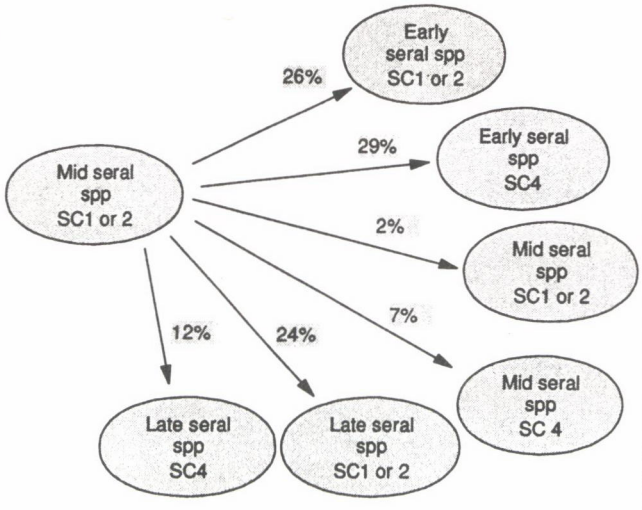
Early-seral spp. are white pine and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir,
Late-seral spp. are largely grand fir.

M332a, HT 5:
Pathways from pines and larch cover type,
in seedling/sapling and pole structure classes.
Percent of hectares, 1935 to 1975.



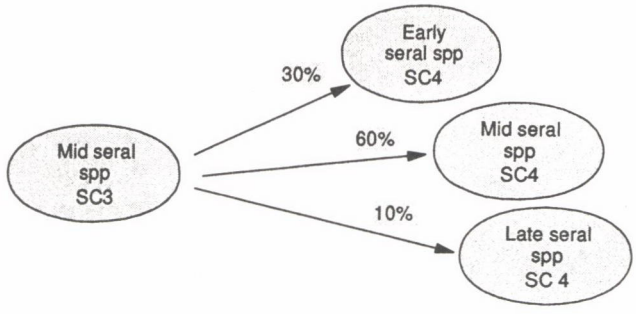
Early-seral spp. are generally ponderosa pine, lodgepole and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir and grand fir,
Late-seral spp. are largely western redcedar and western hemlock.

M332a, HT 5:
Pathways from Douglas-fir and grand fir cover type
in seedling/sapling and pole structure classes.
Percent of hectares, 1935 to 1975.



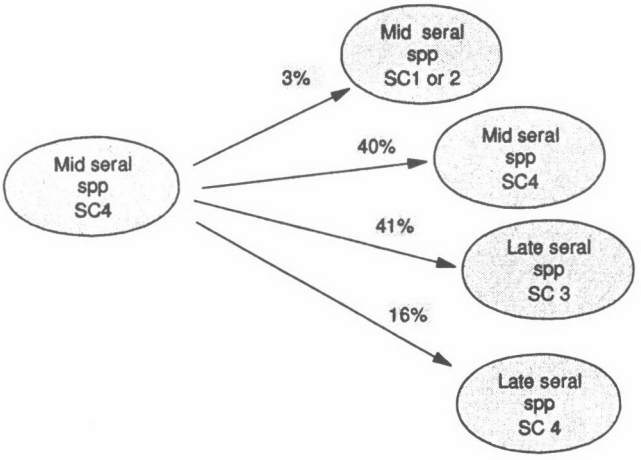
Early-seral spp. are generally ponderosa pine, lodgepole and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir and grand fir,
Late-seral spp. are largely western redcedar and western hemlock.

M332a, Ht 5:
Pathways from Douglas-fir and grand fir cover type,
in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



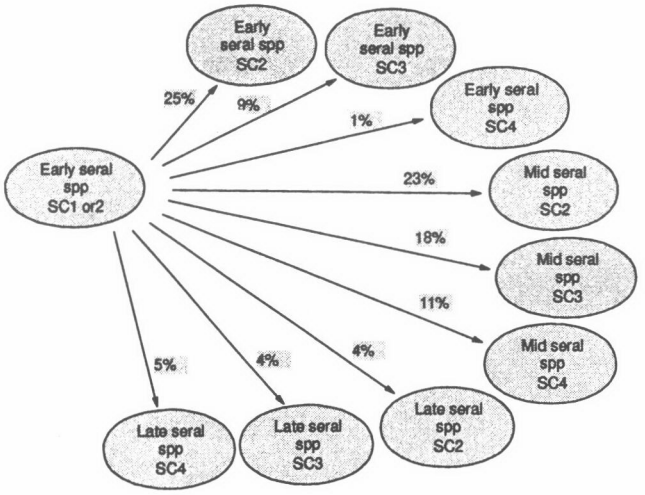
Early-seral spp. are generally ponderosa pine, lodgepole and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir and grand fir,
Late-seral spp. are largely western redcedar and western hemlock.

M332a,HT 5:
Pathways from Douglas-fir and grand fir cover type,
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



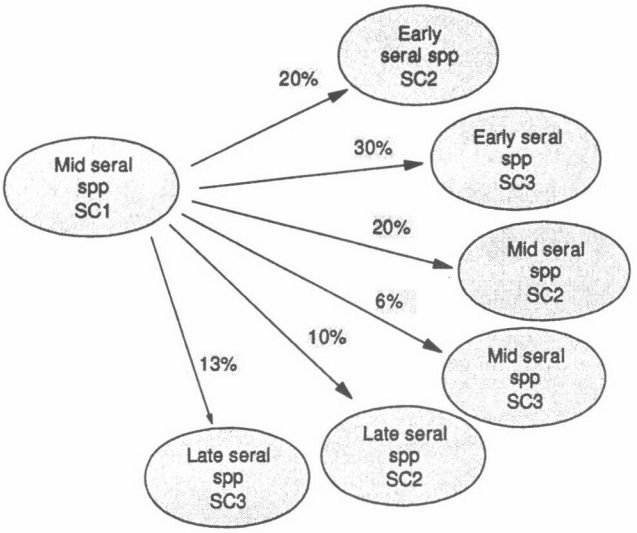
Early-seral spp. are generally ponderosa pine, lodgepole and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir and grand fir,
Late-seral spp. are largely western redcedar and western hemlock.

M333d, HT 5:
Pathways from white pine and larch cover type,
in seedling/sapling and pole structure classes.
Percent of hectares, 1935 to 1975.



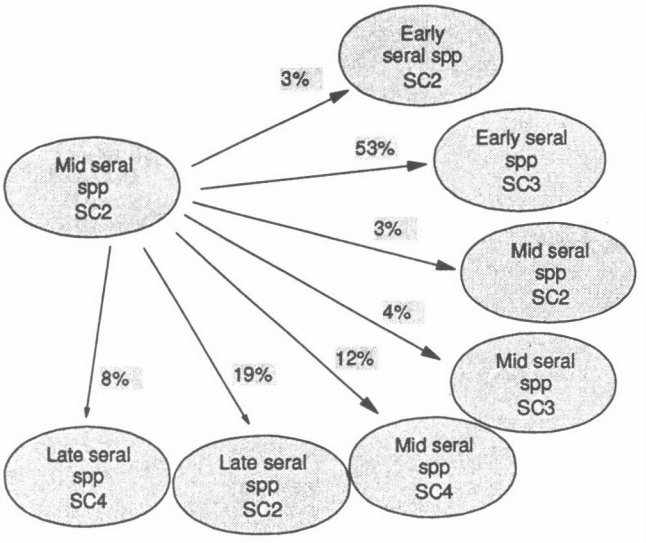
Early-seral spp. are mostly mixtures with white pine or larch,
Mid-seral spp. are primarily Douglas-fir and grand fir,
Late-seral spp. are primarily western redcedar and western hemlock.

M333d, HT 5:
Pathways from Douglas-fir/grand fir cover type,
in seedling/sapling structure class.
Percent of hectares, 1935 to 1975.



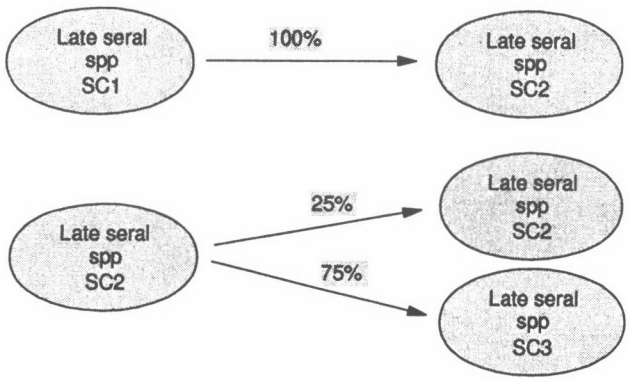
Early-seral spp. are white pine and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir and grand fir,
Late-seral spp. are largely western redcedar and western hemlock.

M333d, HT 5:
Pathways from Douglas-fir/grand fir cover type,
in pole structure class.
Percent of hectares, 1935 to 1975.



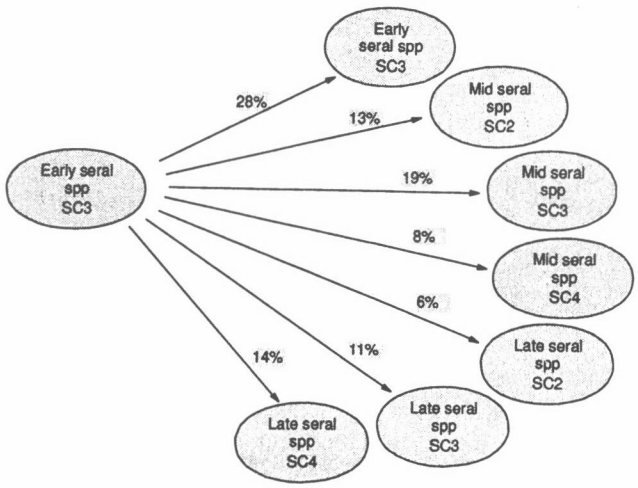
Early-seral spp. are white pine and larch,
Mid-seral spp. are mixtures heavy to Douglas-fir and grand fir,
Late-seral spp. are largely western redcedar and western hemlock.

M333d, HT 5:
Pathways from cedar and hemlock cover type
in seedling/sapling or pole structure classes.
Percent of hectares, 1935 to 1975.



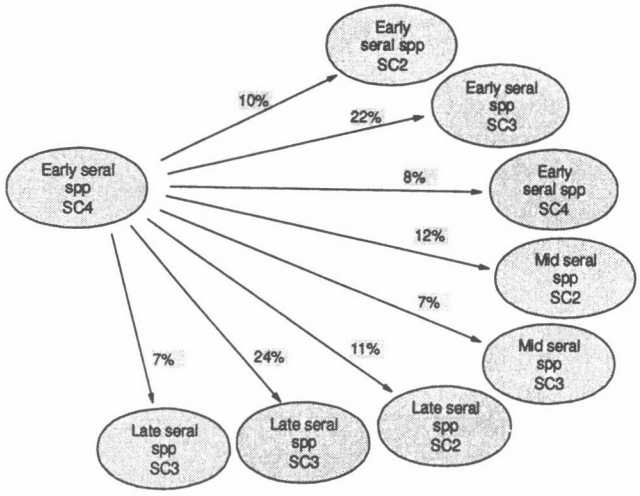
Late-seral spp. are primarily western redcedar and western hemlock.

M333d, habitat type group 5:
Pathways from white pine and larch cover type,
in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



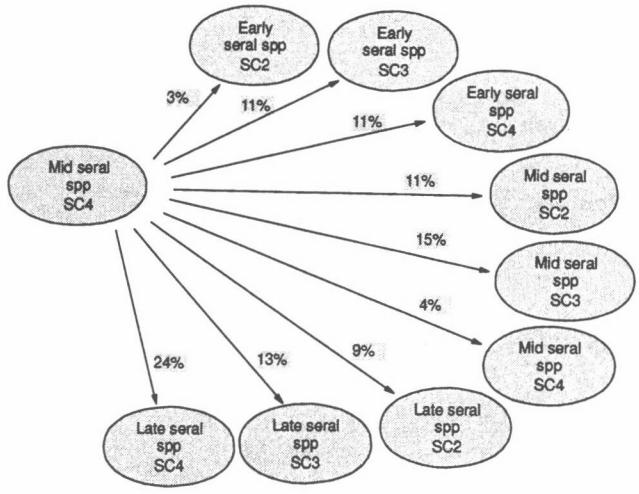
Early-seral spp. are mostly mixtures with white pine or larch,
Mid-seral spp. are primarily Douglas-fir and grand fir,
Late-seral spp. are primarily western redcedar and western hemlock.

M333d, HT 5:
Pathways from white pine and larch cover type,
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



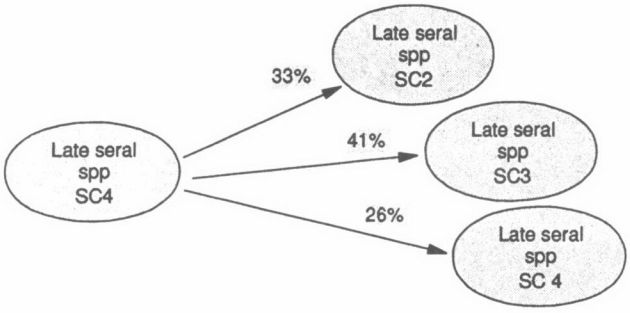
Early-seral spp. are mostly mixtures with white pine or larch,
Mid-seral spp. are primarily Douglas-fir and grand fir,
Late-seral spp. are primarily western redcedar and western hemlock.

M333d, HT 5:
Pathways from Douglas-fir/grand fir cover type
in large-tree, open canopy structure class.
Percent of hectares, 1935 to 1975.



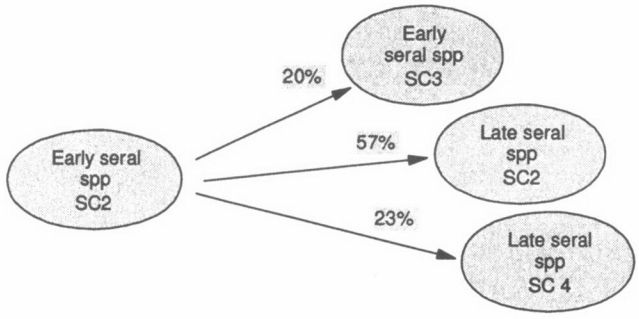
Early-seral spp. are mostly mixtures with white pine or larch,
Mid-seral spp. are primarily Douglas-fir and grand fir,
Late-seral spp. are primarily western redcedar and western hemlock.

M333d, HT 5:
Pathways from western redcedar and western hemlock cover types in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



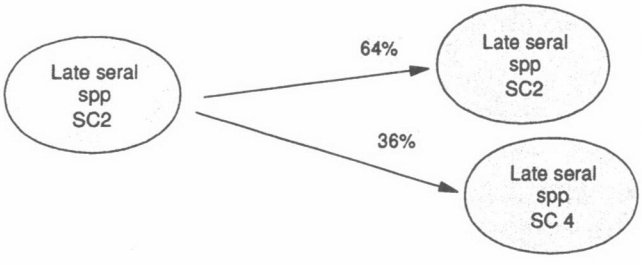
Late-seral spp. are largely western redcedar and western hemlock.

M332a, HT 7:
Pathways from pine and larch cover type in pole structure class.
Percent of hectares, 1935 to 1975.



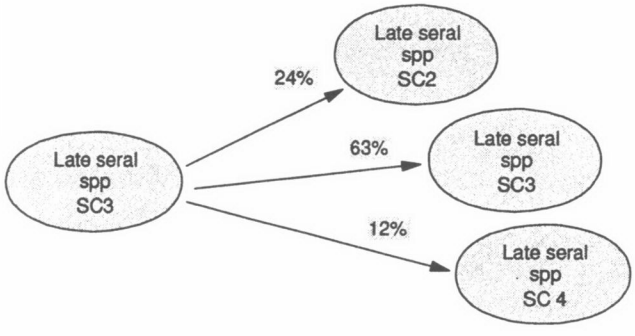
Early-seral spp. are generally mixtures with lodgepole pine or western larch, Late-seral spp. are generally Douglas-fir and subalpine fir.

M332a,HT 7:
Pathways from Douglas-fir and subalpine fir cover type in pole structure class.
Percent of hectares, 1935 to 1975.



Late-seral spp are generally Douglas-fir and subalpine fir.

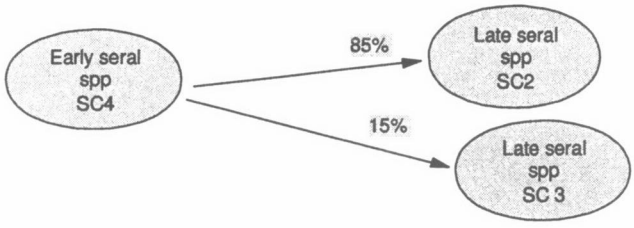
M332a, HT 7:
Pathways from Douglas-fir and subalpine fir cover types in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



Late-seral spp. are generally Douglas-fir and subalpine fir.

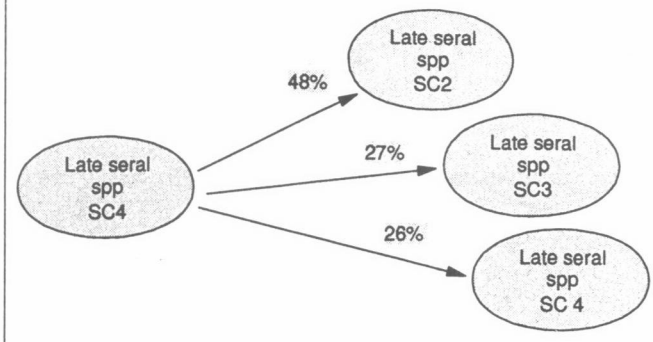
Appendix A: Successional Pathways with Moderate to High Root Disease Influence

M332a, HT 7:
Pathways from Douglas-fir and subalpine fir cover type in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



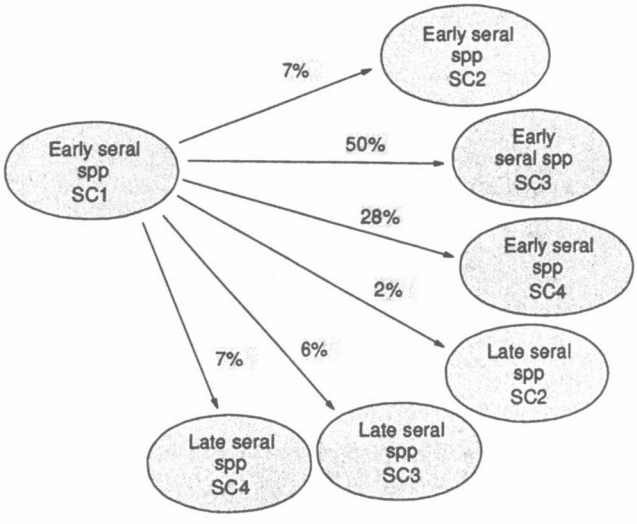
Early-seral spp. are generally mixtures with lodgepole pine or western larch,
Late-seral spp. are generally Douglas-fir and subalpine fir.

M332a, HT 7:
Pathways from Douglas-fir and subalpine fir cover type in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



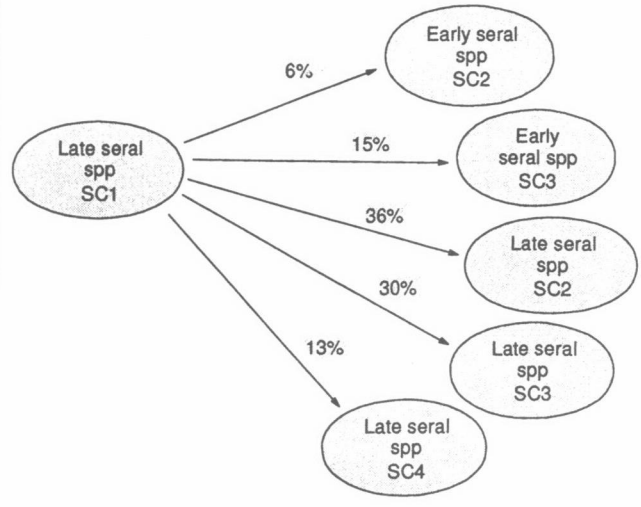
Late-seral spp. are generally Douglas-fir and subalpine fir.

M333d, HT 7:
Pathways from pines and larch cover type in seedling/sapling structure class.
Percent of hectares, 1935 to 1975.



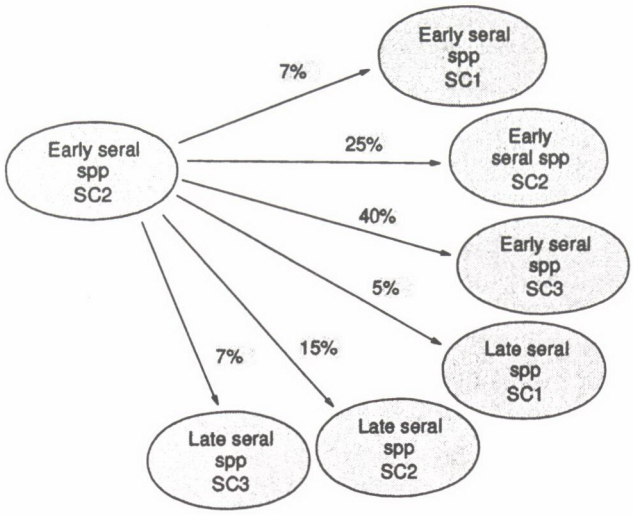
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7:
Pathways from subalpine fir cover type, in seedling/sapling structure class.
Percent of hectares, 1935 to 1975.



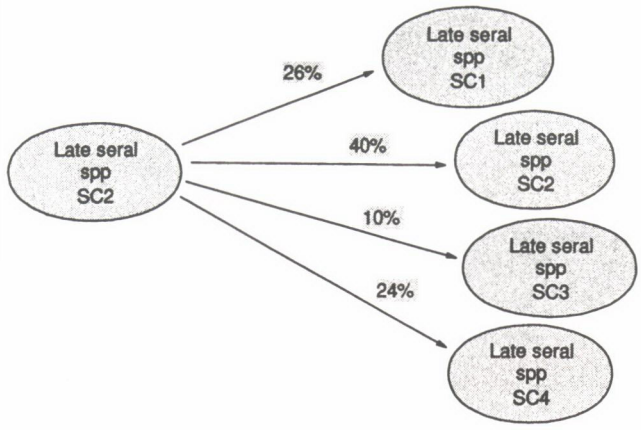
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7:
Pathways from pines and larch cover type,
in pole structure class.
Percent of hectares, 1935 to 1975.



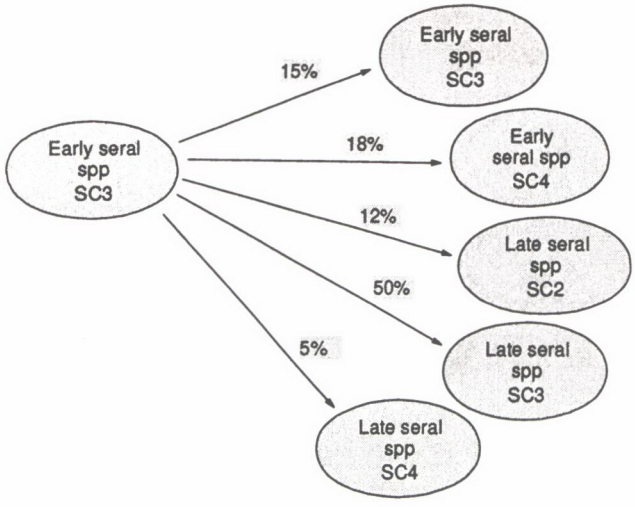
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7:
Pathways from subalpine fir, Douglas-fir and
Engelmann spruce cover type
in pole structure class.
Percent of hectares, 1935 to 1975.



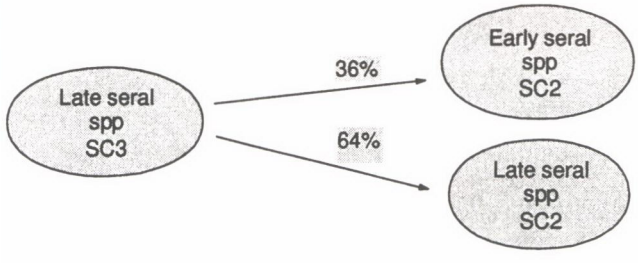
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7:
Pathways from pines and larch cover type
in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



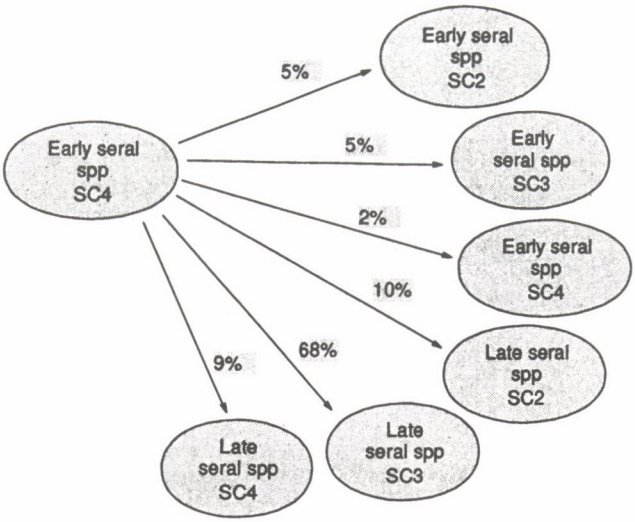
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7:
Pathways from subalpine fir cover type,
in large-tree, closed canopy structure class.
Percent of hectares, 1935 to 1975.



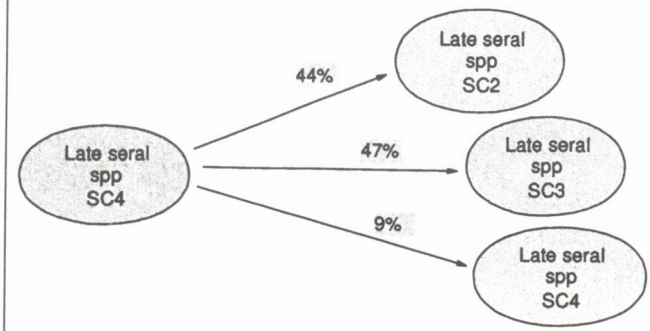
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7:
Pathways from pines and larch cover type
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



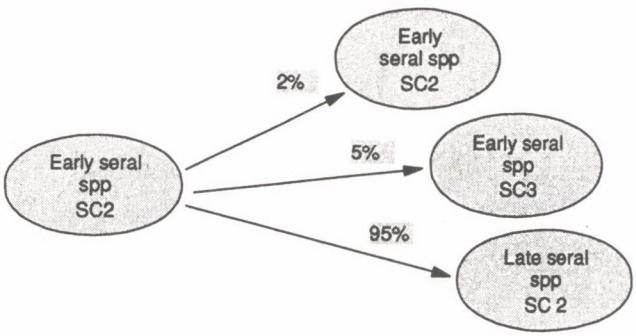
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 7: .
Pathways from subalpine fir, Douglas-fir and
Engelmann spruce cover type
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.



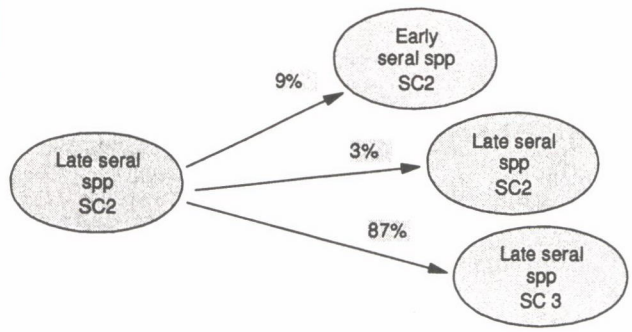
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M332a, HT 9:
Pathways from pine and larch cover type,
in sapling to pole structure class.
Percent of hectares, 1935 to 1975.



Early-seral spp. are generally pines, and larch,
Late-seral spp. are subalpine fir, Douglas-fir and spruce.

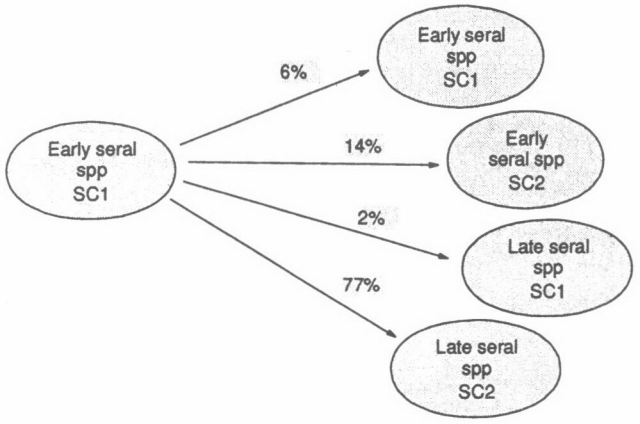
M332a, HT 9:
Pathways from Douglas-fir, spruce
and subalpine fir cover type
in sapling to pole structure class.
Percent of hectares, 1935 to 1975.



Early-seral spp. are generally pines, and larch,
Late-seral spp. are subalpine fir, Douglas-fir and spruce.

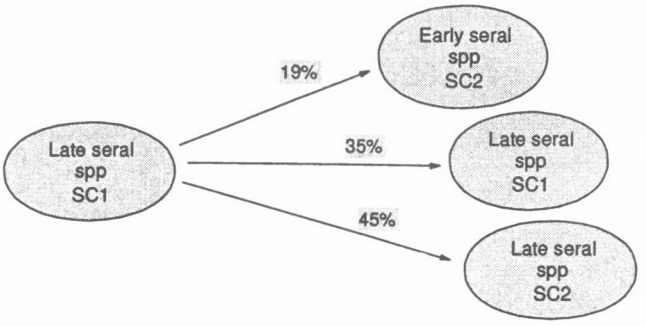
Appendix A: Successional Pathways with Moderate to High Root Disease Influence

M333d, HT 9:
Pathways from white pine, lodgepole pine and western larch cover types
in seedling/sapling structure class.
Percent of hectares, 1935 to 1975.



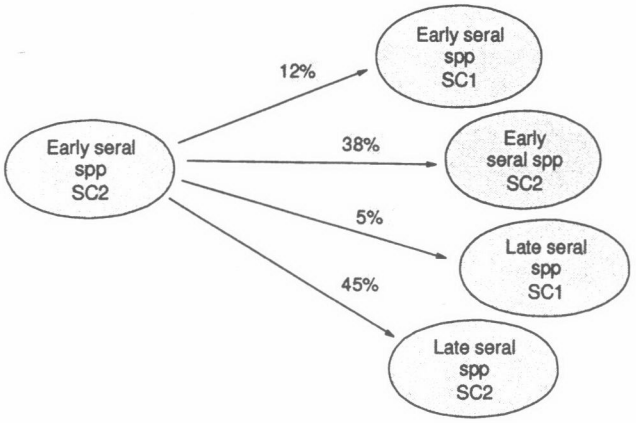
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 9:
Pathways from subalpine fir, Douglas-fir and Engelmann spruce cover types
in seedling/sapling structure class.
Percent of hectares, 1935 to 1975.



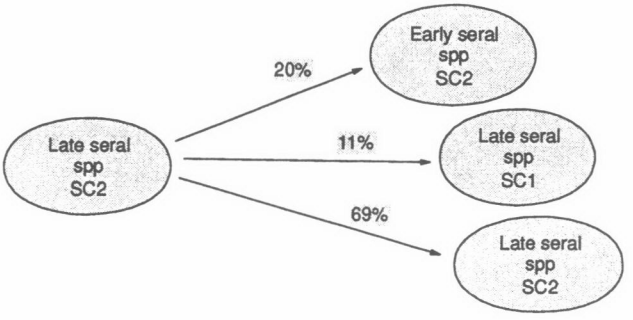
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

M333d, HT 9:
Pathways from white pine, lodgepole pine and western larch cover types
in pole structure class.
Percent of hectares, 1935 to 1975.



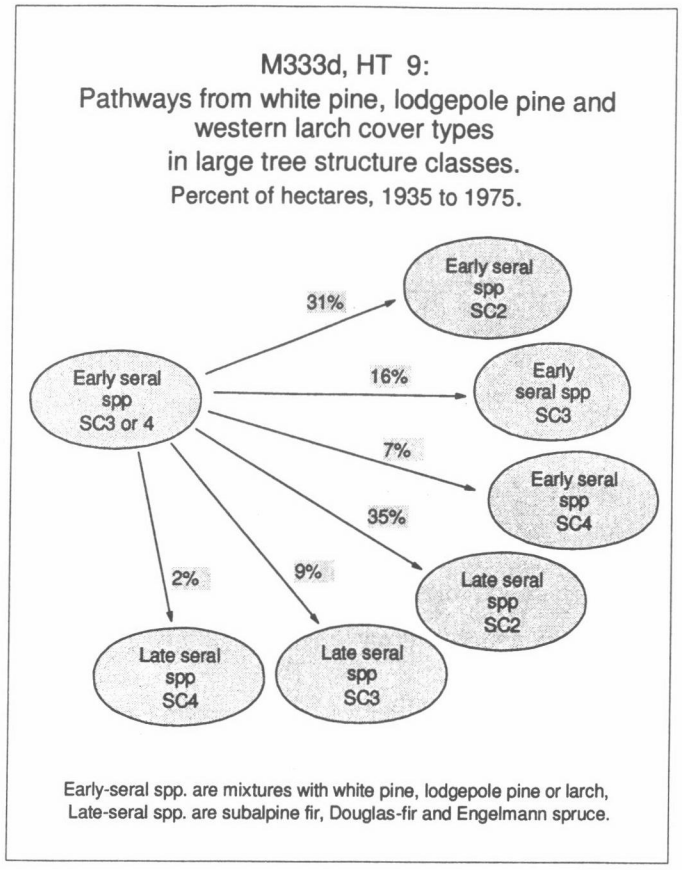
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

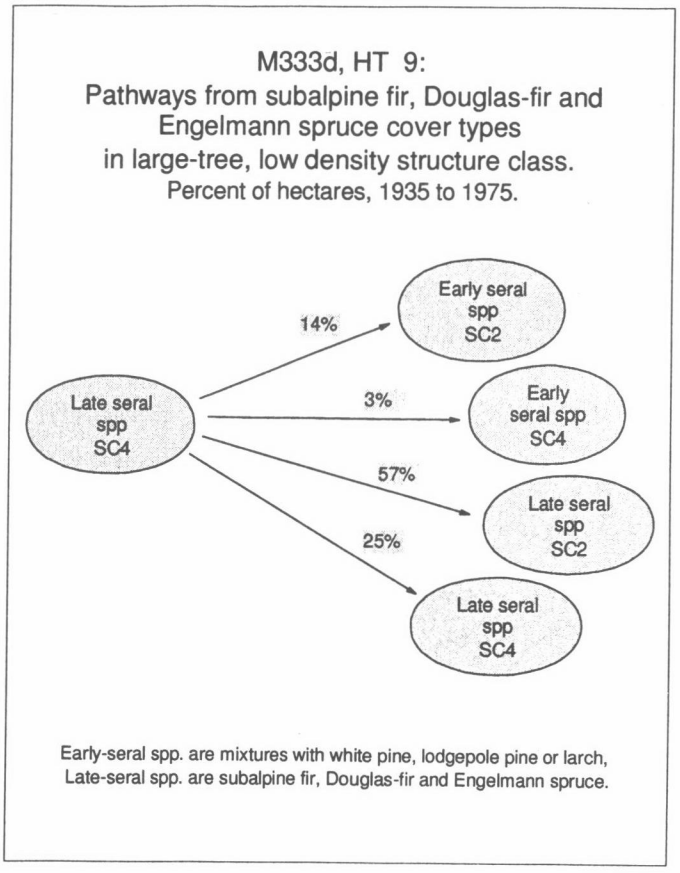
M333d, HT 9:
Pathways from subalpine fir, Douglas-fir and Engelmann spruce cover types
in pole structure class.
Percent of hectares, 1935 to 1975.



Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

Appendix A: Successional Pathways with Moderate to High Root Disease Influence


M333d, HT 9:
Pathways from white pine, lodgepole pine and western larch cover types
in large tree structure classes.
Percent of hectares, 1935 to 1975.
Early seral spp SC3 or 4
31%
Early seral spp SC2
16%
Early seral spp SC3
7%
Early seral spp SC4
35%
Late seral spp SC2
2%
9%
Late seral spp SC4
Late seral spp SC3
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.


M333d, HT 9:
Pathways from subalpine fir, Douglas-fir and Engelmann spruce cover types
in large-tree, low density structure class.
Percent of hectares, 1935 to 1975.
Late seral spp SC4
14%
Early seral spp SC2
3%
Early seral spp SC4
57%
Late seral spp SC2
25%
Late seral spp SC4
Early-seral spp. are mixtures with white pine, lodgepole pine or larch,
Late-seral spp. are subalpine fir, Douglas-fir and Engelmann spruce.

APPENDIX B: TABLES OF CONTENTS, VOLUME 1 AND SUMMARY

Hagle, S.; T. Johnson; M. Marsden; L. Lewis; L. Stipe; J. Schwandt; J. Byler; S. Kegley; C. Bell Randall; J. Taylor; I. B. Lockman; N. Sturdevant; S. Williams. 2000. Successional Functions of Pathogens and Insects; Ecoregion Sections M332a and M333d in Northern Idaho and Western Montana. Volume 1: Methods. Region 1 FHP Report 00-10. Missoula, MT: USDA Forest Service, State and Private Forestry, Cooperative Forestry and Forest Health Protection, Northern Region. 101 p.

Byler, J. and S. Hagle. 2000. Successional Functions of Pathogens and Insects; Ecoregion Sections M332a and M333d in Northern Idaho and Western Montana: Summary. Region 1 FHP Report 00-09. Missoula, MT: USDA Forest Service, State and Private Forestry, Cooperative Forestry and Forest Health Protection, Northern Region. 39 p.

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